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STUDIES ON THE MORPHOLOGY AND LIFE HISTORY OF NEMATODES IN THE GENUS SPIRONOURA

WITH FIVE PLATES AND TWO TEXT-FIGURES

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I. INTRODUCTION

Few extensive studies have been made on the anatomy and growth variations of nematodes, and these have been confined so largely to isolated and economic forms that nothing like a comprehensive knowledge of the group as a whole is available. Thus it has been deemed worth while to extend our knowledge through study of a form not too nearly related to the Ascarids, Oxyurids, and Ancylostomas, already well known.

Extensive collections of several species of the genus Spironoura have provided sufficient material to make such studies possible. Species of this genus are almost constant inhabitants of the posterior alimentary canal of various species of turtles. Most of the collections were made in Oklahoma.

Because I have come to the conclusion that the separation of families, subfamilies, and genera should depend primarily upon the variations in the digestive and reproductive systems, I have placed greatest emphasis on the study of these two systems. When speaking of the reproductive system, I mean the genital tubes. I believe that male secondary organs, such as spicules, gubernaculum, and caudal papillae have been made to bear a disproportionately great part in diagnoses of groups of these ranks. Until general knowledge of fundamental types of the major systems is made available, our taxonomic schemes must remain unnatural and more or less makeshift.

In addition to the structural studies, taxonomic studies have been made on the North American species of Spironoura, and a key compiled for ready determination.

I am indebted to Dr. Henry B. Ward for much encouragement and criticism during the work, and take this opportunity to express my appreciation. I also am indebted to him for the loan of slides and specimens, and for the use of his extensive personal library.

II. ANATOMY

Spironoura chelydrae (Harwood) 1932

General External Morphology

The genus Spironoura belongs in the family Kathlaniidae Travassos, and to the subfamily Kathlaniinae. The family is one of the oxyuroid groups containing reptilian parasites for the most part and including several species parasitic in fishes and amphibians. Spironouran species are found parasitic in representatives of all three groups, but are primarily

and characteristically parasitic in turtles. From North America at the present time eight species have been described, and two more to be described in this paper bring the total number of species to ten. Each of these will be discussed later.

The species *S. chelydrae* was chosen for an extended anatomical study for several reasons. I believe the species to be representative of one of those groups which have become parasitic only recently, relatively speaking, as evidenced by the position within the host (rectum) which is close to one of the portals of entry. The medium within which these worms live is not so very different from the habitat of some free-living species which live in fresh or decaying dung. Specimens of Spironoura live for the most part in the feces of the host and feed upon this material, as evidenced by studies of the intestinal contents. Moreover, anatomically the group is not far distant from Rhabditidae, a family composed of both free-living and parasitic species.

The species was described by Harwood (1932). His description is rather brief, and the single drawing (of the tail of a male) decidedly sketchy. He placed the species in the genus Falcaustra Lane, which I consider a synonym of Spironoura.

Morphology.—The form of the worms may be seen in Figs. 3 and 12. Specimens fixed in hot fluids never straighten entirely, because in the male there are accessory ventral muscles, and in the female the ventral somatic muscles are a little wider than in the dorsal sectors. Thus in the male the "lateral" lines are somewhat dorso-lateral. The body tapers to a point posteriorly and anteriorly; the head, however, although much smaller in diameter than the middle region, is bluntly truncate (Fig. 20). The female is distinctly narrower posterior to the vulva than anteriorly. Only a small portion of the reproductive system extends posterior to the vulva. The tail in both sexes is sharply pointed and is shaped like a narrow cone. In the female it is apt to be nearly straight; in the male it is always more or less curved ventrally in fixed specimens, the amount of curvature depending upon the temperature of the fixative. Some specimens may be merely curved as in Fig. 12, while others are spirally coiled with two or three loops. Complete measurements are given in Tables 1 and 4.

A cross section in the middle trunk region is not circular. The worms in the middle region of the body have a greater dorso-ventral diameter than transverse, being laterally flattened. This may be an effect of fixation, but it is constant in all specimens I have sectioned.

In the male, just anterior to the anus is a pair of longitudinal trough-like depressions (Fig. 10). The median preanal papilla is situated on a narrow ridge separating the two grooves. This is apparently a specific

character, since it is not found in other species. In the female, only a single depression is present in this region, the separating ridge being absent.

The head bears three low lips, one dorsal, the other two subventral (Figs. 17 and 20). There are four papillae to each lip, two internal and two external. All of these are of the sessile type.

In addition to the papillae the two subventral lips each bear an amphid (Fig. 17). These structures have not been hitherto reported for Spironoura. They are situated laterally, each very close to one of the papillae. In anterior view they appear as smooth convex circular areas, with a transverse slit across the middle. They are observable in ventral views of the head also (Figs. 20, 60, 64, etc.).

The cervical papillae are situated laterally, far back from the head (1.1 mm.) just anterior to the level of the anterior end of the excretory bridge.

The male has 10 pairs of caudal papillae and an unpaired median preanal papilla. The arrangement of these is shown in Fig. 10. Two pairs are lateral, both postanal, one immediately posterior to the level of the anus, and one farther back (numbers 3 and 4, respectively). The remainder are subventral. Two pairs of these are postanal, situated near the level of the posterior lateral pair (Fig. 10, numbers 1 and 2). Three pairs are circum-anal (numbers 5, 6, and 7). Usually all of these are

TABLE 1.—MEASUREMENTS OF APPROXIMATELY MAXIMUM AND MINIMUM MATURE SPECIMENS (IN MILLIMETERS)

Spironoura chelydrae (Harwood) 1932

Females	Minimum	Maximum	Males	Minimum	Maximum
Total length	9.5	22.55	Total length	6.65	16.3
Greatest breadth	0.47	0.89	Greatest breadth	0.32	0.66
Head breadth	0.09	0.18	Head breadth	0.08	0.16
Breadth at anus	0.20	0.47	Breadth at anus	0.18	0.46
Pharynx length	0.08	0.10	Pharynx length	0.07	0.10
Pharynx breadth	0.08	0.12	Pharynx breadth	0.06	0.10
Cylindric esophagus length	1.24	1.84	Cylindric esophagus length	1.60	1.79
Cylindric esophagus breadth	0.10	0.15	Cylindric esophagus breadth	0.08	0.13
Anterior bulb length	0.18	0.30	Anterior bulb length	0.13	0.25
Anterior bulb breadth	0.10	0.18	Anterior bulb breadth	0.08	0.17
Posterior bulb length	0.17	0.29	Posterior bulb length	0.14	0.26
Posterior bulb breadth	0.18	0.29	Posterior bulb breadth	0.16	0.27
To excretory pore	1.22	1.98	To excretory pore	0.86	1.82
To nerve ring	0.34	0.47	To nerve ring	0.28	0.46
Rectum length	0.20	0.53	Cloaca length	0.18	0.49
To vulva	6.23	13.68	Sucker to anus	1.87	4.60
Vagina length	2.44	4.82	Spicule length	2.35	4.50
Tail length	0.66	1.64	Tail length	0.40	1.00
Eggs length	0.099	0.105	Gubernaculum length	0.14	0.20
Eggs breadth	0.059	0.072			

slightly posterior to the anus, but one of them is sometimes anterior to the level of the anus. It seems better, therefore, to designate these as circum-anal to avoid confusion resulting from variability. The last three pairs are preanal. One of these is situated at about the level of the anterior end of the cloaca (number 8), the next pair 0.26 mm. anterior to this one, and the last pair 0.35 mm. anterior to the latter in an 11-mm. male (numbers 9 and 10 not shown in Fig. 10).

While the oblique muscles of the male are not external structures they are visible even in some uncleared specimens and should be mentioned. The obliques begin just anterior to the anus and extend forward about a fourth of the body length. The pseudo-sucker is similarly situated just anterior to the obliques, and consists of a pair of fan-shaped muscular areas.

Lip Supports

Special consideration is given to the lip supports because they have been so generally misrepresented, because they afford such a definite character binding the various species of the genus Spironoura, and because in variational details they afford characters of specific value. In following the description, reference should be made to Figs. 17, 20, 57, etc.

The support is generally said to be cuticular, which is correct only if taken to mean that it is composed of a hard, homogeneous substance, non-nucleated and perhaps of the nature of a secretion. If the term *cuticular* is taken to mean that the support is of the same substance as the body-wall cuticula, it is probably used incorrectly. There is reason to believe that several so-called cuticular structures, such as the gubernaculum, the spicules, and the lip support, which are internal and not derived from the proctodeum or stomodeum, are composed of an entirely different substance from the body-wall cuticula. The data from staining reactions tend to support this view.

The ring support of the lips, as the name implies, is a ring composed of a hard substance encircling the lips; it affords an immovable point of origin for the muscles of the lips, as well as for parts of the anterior somatic musculature, the pharyngeal muscles, and the papillae tubes; and it serves to bind together the angles of the lips, this function being perhaps the least significant of all. The structure is not a thickening of the head cuticula, but rather an internal structure in its entirety (Fig. 52), a point on which several authors have been in some confusion (Walton, 1930).

The "ring" is not circular but tends to be more or less hexagonal. Each angle of the hexagon is modified and thickened. I call these thickenings the *nodes* of the support. There are two types of nodes: those found at the angles of the triangular vestibule, and those in the middle

region of each lip. The latter I refer to as the *pharyngeal supports,* from their principal function, and the former as the *angle supports,* from their position. Between each angle support and the adjacent pharyngeal support on each side, there are flattened bars, somewhat curved inwardly, to which I refer as the *connecting bars.*

Each angle support consists of an irregular piece (Figs. 17, 20, and 57) curving somewhat around the angles of the vestibule, with connecting bars projecting laterally on each side to the pharyngeal supports, and with a single triangular piece projecting posteriorly which makes contact with the angle of the pharyngeal cuticula lying in the same radius. This latter piece is specifically characteristic in surface view (Fig. 20). Muscle attachments to the angle supports consist only of fibres from the somatic muscles.

Each pharyngeal support lies in the center of a lip. It consists of a flattened anterior piece, with the lateral connecting bars projecting on each side, and a posterior piece in which the origins of some of the anterior pharyngeal muscles are found. The anterior plate affords a firm point of origin for the lip muscles (Fig. 52) which are attached in a row to the anterior surface, and spread fan-wise to the internal and anterior surfaces of the lips. Lip movement is accomplished by these muscles. The anterior plate also affords firm attachment for fibres from the somatic muscles. The posterior part of the pharyngeal support fits against the posterior surface of the anterior plate. Its own posterior and internal surface is deeply concave to accommodate the rounded surface of the anterior radial muscles of the pharynx which have their origin in it. The pair of backwardly projecting arms (formed by the posterior concavity) connect with the tunica propria of the pharynx.

To the connecting bars are attached the tubes of the papillae, which pass around the bars on the outside, lying in the concavities between nodes.

I believe it is clear that the type of support described by Baylis and Daubney for the genus Zanclophorus is closely related to that of Spironoura, if not identical with it. The horseshoe-shaped supports for the angles of the lips described by them are undoubtedly what I refer to in this paper as the angle supports. I should be very much surprised if further investigation does not reveal that the pharyngeal supports and connecting bars are present in Zanclophorus also. I might point out that *S. chelydrae,* were it not for the nature of the lip supports and papillae, would be practically identical in all other generic characters to Zanclophorus. The only North American species referred to Zanclophorus is Walton's *Z. cryptobranchi,* which I have determined by study of the type specimens is an undoubted Spironouran. Since I prefer to limit my

studies as much as possible to North American species, I do not feel justified in making any final conclusion concerning the validity of the genus Zanclophorus.

A note concerning the structure of the median strands of the lateral lines may be inserted here. These structures (Figs. 16, 18, 19) are certainly not of the same tissue as the lateral strands. There are several evident differences. First, the nuclei are larger and much less numerous in the median strands and form a single row down the length of the body. Secondly, the cytoplasm has marked dissimilarities as shown by staining reactions. Lastly, the median strand is not a syncytium. The cell boundaries, as definite walls, are clearly depicted in tangential sections. The cell shape is that of an oblong rectangle, with the long axis coinciding with that of the body. The strands are each composed of a single row of cells. Some free-living nematodes have been found to correspond to this condition, which I take to be primitive.

Digestive System

In Spironoura the digestive system consists of five parts. These are, naming from anterior to posterior, (1) vestibule, (2) pharynx, (3) esophagus, (4) intestine, and (5) proctodeum (Fig. 3). I am using the nomenclature of Yorke and Maplestone (1926) in this paper.

The vestibule is that portion of the digestive tract bounded by the lips (Figs. 17 and 52). A cross section has the shape of an equilateral triangle. Its depth is shallow, about 20 to 30 μ, depending somewhat on the state of contraction of the lips. The posterior boundary is the anterior surface of the muscles of the pharynx. The cuticula of the vestibule is not, however, continuous into the pharynx, and staining reactions indicate that the lining in the two parts is of somewhat different substance. The anterior edges of the three lips, which form the anterior boundaries of the vestibule, bear thickened transverse ridges, wider in the center of the lips. In longitudinal section these appear as blunt lobes (Fig. 52). Just posterior to these ridges is a second similar set of transverse ridges, rather more sharply edged than the anterior ones. These are the structures, illustrated in many figures of the head of species of Spironoura, that appear to be inwardly directed triangular points set in the middle of each lip. They actually represent optical sections of the ridges. The relative prominence of the ridges and the angle assumed in relation to the longitudinal axis of the body depend on the degree of contraction of the lips.

The pharynx is a short region bounded anteriorly by the vestibule and posteriorly by the esophagus (Figs. 20 and 47). The total length is about 0.08 mm., measuring the length of the muscles, and the width (ventral

view) is 0.75 mm. The pharynx is distinctly different, both as to lining and musculature, from the esophageal region.

The lumen, often spoken of as wide or narrow, is wide or narrow in proportion to the degree of contraction of the muscles. The breadth of the lumen is not, therefore, a taxonomic character, although given in some generic and specific diagnoses. A cross section is triangular or tri-radiate, the angles of the lumen are bluntly acute, and the middle of each flat surface has an inwardly projecting blunt ridge, running the length of the pharynx. The shape of the lumen is shown in Fig. 47.

The lining is thick and obviously composed of two layers. At the angles of the lumen the two layers are discrete, since they must slide upon each other when the pharynx is opened or closed. The primary or inner layer is thinner than the secondary layer, and is continuous all the way around, while the secondary layer is interrupted in the middle of each muscle field, allowing insertion of the large surface muscles to the primary cuticula. The median ridges are produced anteriorly into the basal region of the vestibule, not as sharp teeth, but as flat plates, to form a grinding organ. In longitudinal section, they appear as teeth. These are the "cuticular fringes" of Baylis and Daubney (1922).

Angle muscles are absent in the pharynx. The angles of the lumen are attached directly to the tunica propria (Fig. 47). The three sets of surface muscles are each composed of four units, as follows: one anterior median muscle, inserted in the middle of the field, with its origin on the pharyngeal supports of the lip support ring. A second muscle also lies in the median line directly posterior to the first. The origin of this one is in the tunica. It extends to the posterior end of the pharynx. On either side of the two median muscles is a flat muscle, forming flanking units of the median set. These are thicker and heavier anteriorly than posteriorly. They disappear entirely before reaching the posterior end of the pharynx. All muscles but the anterior medians are shown in Fig. 47.

No nuclei of any kind are to be found in the pharyngeal muscles.

The esophagus consists of an anterior cylindrical portion of nearly equal diameter throughout, and a posterior bulb equipped with a corrugated valve and intestinal valve (cardia) (Fig. 3). The bulb is divided into two unequal parts by a deep constriction, giving an "hourglass" effect in some species. The musculature of the bulb (including both parts) and that of the cylindrical esophagus are distinctly different structures, so that the division is not an artificial one.

The lumen presents a different picture in different parts of the esophagus. In the cylindrical portion it is regularly tri-radiate in cross section with a widening at the angles. This widening is characteristic of this section and absent in the bulb. It represents a longitudinal canal, one

at each angle of the lumen (Fig. 18). The central lumen is in communication with the canals along their entire length. In the anterior bulb, as stated, the accessory canals are absent. Here the angles of the lumen are very acute, and a cross section is more nearly perfectly triangular (Fig. 16). This condition is retained into the posterior bulb. At the corrugated valve the entire lumen abruptly widens, so that the walls of the anterior end stand at right angles to the longitudinal axis. Cross sections would here be tangential to the walls, giving the peculiar appearance shown in Fig. 41. The angles of the lumen are more pronouncedly extended than the intermediate regions, for attachment of muscles. The posterior walls of the valve do not narrow so abrubtly, but taper gradually to the intestinal valve, just anterior to which the typical tri-radiate appearance is seen in cross section (Text-fig. 1, j).

It is necessary to point out that the so-called corrugated valve neither is extraordinarily corrugated nor is it a valve. It is a chamber, which, by manipulation of special muscles may have its cubic capacity increased or decreased. It represents a simple dilation of the lumen and is not a true valve, since there is no mechanism for prevention of regurgitation. Dilation of the walls would tend to draw materials into it, which would without further manipulation pass into the intestine. The corrugated valve is then of the nature of a suction pump, and the valve to prevent backflow is at the entrance to the intestine (the cardia).

The cuticula of the entire esophagus is equipped with special thickenings on the external surface for the insertion of the muscles. These are especially strongly developed on the surfaces of the corrugated valve.

Three pointed projections in the form of teeth are found at the anterior end of the cylindrical esophagus. These are in the center of each surface field, and are directed forward into the lumen of the pharynx.

A description of the muscles of the cylindrical esophagus is comparatively simple. The angle muscles are attached to the external surfaces of the accessory canals, some of the fibres passing around to the sides. There are two longitudinal rows of fibres to each angle of the lumen. They may be separated from the surface muscles by the slightly deeper staining reaction (Fig. 18). Of the surface muscles there are apparently eighteen rows, six to each field, but the fibres at any one cross section are hardly separable except at their insertions in the thickenings of the cuticular lining. The bundles are more evidently discrete in longitudinal section. These rows extend the entire length of the cylindrical esophagus. The esophageal glands divide the rows into two groups of three each in each muscle field (Fig. 18). Probably the division of the surface muscles into small bundles of fibres has no other significance than as an adaption for more secure insertion. Modifications of the musculature of the anter-

ior bulb and the anterior third of the posterior bulb consist, first, in the insertion of the angle muscles in the acute point of the angles of the lumen, in the absence of the accessory canals; secondly, in resolving the two rows of the angle muscles into one, possibly a result of crowding; and, thirdly, in the union of each of the three rows of surface muscles of each half-field into a single row. Fig. 16 shows the condition of the muscles here.

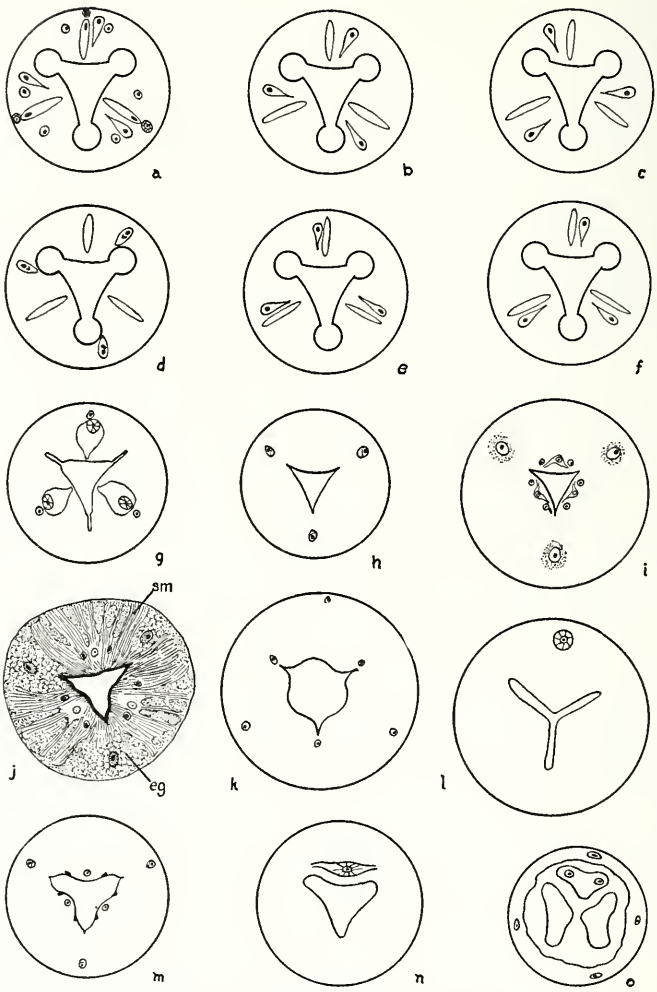
A very complicated series of modifications has taken place in the muscles of the posterior bulb, correlated with the modifications of the lumen into the corrugated valve. In spite of the extensive modifications, all the muscles may be referred to either the angle muscles or the surface muscle type. The bundles of both are divided into anterior and posterior groups, which for the most part have their insertions in the extreme angles or widest part of the surfaces of the corrugated valve. Contraction of the anterior bundles shifts the valve forward and closes the lumen. Muscles of the cardia close the valve into the intestine at the same time. Contraction of the posterior bundles opens the corrugated valve to its widest extent and pulls the entire structure backward, thus producing a suction. The cardia open at the same time, allowing food to enter the intestine. These movements have been observed in living animals. Figs. 40 and 49 show distribution of the muscles.

Muscle Nuclei of the Esophagus.—For convenience the discussion treats the nuclei of the cylindrical esophagus and the bulb separately. The former will be discussed first.

Pertaining to the muscles, there are three types of nuclei, differing in form and staining reaction. The first of these is in the form of the conventional tear-drop (Fig. 39). The acute point is sometimes drawn out into a long thread, which is always directed toward the center of the lumen. Thus the long axis of the nuclei always corresponds to one of the radii of the esophagus as seen in cross section. A single large nucleolus occupies the large end, and sometimes other chromatic elements are present. The length is 19 μ, the breadth 8 μ, the nucleolus being about half the breadth.

The second type of nucleus of the cylindrical esophagus presents no special features. The nuclei are small, oval, or spherical, with a small central nucleolus. The diameter is 6 μ. These nuclei stain rather lightly, and are apt to be overlooked because of their small size (Fig. 42). The third type resembles the tear-drop type, but is more nearly oval, and has an additional odd-shaped nucleolus (Fig. 37).

The distribution of the nuclei is as follows: The first set is at a level between 10 and 40 μ posterior to the junction of the pharynx and esophagus, i.e., in the extreme anterior end. The nuclei and their positions are



TEXT-FIG. 1.—Diagrams *a* to *f*, inclusive, show muscle nuclei of the cylindrical esophagus. Radially striated cells and those in the gland ducts belong to the sympathetic nervous system. *g*, nerve cells and muscle cells of the anterior bulb. *h*, angle muscle nuclei of the anterior region of the posterior bulb. *i*, esophageal gland nuclei (over the angles), nerve cells (median surface fields); surface muscle nuclei in the middle of the half-fields. *j*, same as *i*, drawn in detail with camera lucida. *k*, third set of muscle nuclei. *l* and *n*, nerve nuclei. *m* and *o*, fourth set and cardial set of muscle nuclei.

illustrated in Text-fig. 1, a. The smallest of the nuclei here (lying in and above the esophageal glands) belong to the sympathetic nervous system. There are six of the small round nuclei (type 2), one in the center of each half-field of the surface muscles. These are not all at exactly the same level, since the figure is a combination of five 10 μ sections. This set completes the list of type 2 nuclei of the cylindrical esophagus. The question of their relation to the muscles is uncertain, except that they belong to the surface muscles, and perhaps originally belonged to the pharyngeal group.

At the same level with these six small nuclei is one set of three tear-drop nuclei (type 1). Before proceeding further, I must point out that no two of these occupy the same radius. This first set of three is located, one in each left half of the surface fields, close to the median esophageal glands, excepting the nucleus in the right submedian field which is closer to the angle of the lumen (Text-fig. 1, a). When I say left half or right half of a field it must be kept in mind that I am looking at each sector as if it were dorsally located, i.e., from the lumenward side. Since the sections are seen from the surface, "right" will correspond to the observer's left.

The second set of tear-drop nuclei is situated just posterior to the nerve ring, and about 0.3 mm. from the anterior end of the cylindrical esophagus (Text-fig. 1, b). These are located in each left half of each surface field, about midway between the angle of the lumen and the gland.

The third set is at a level about 0.38 mm. from the anterior end and thus 0.08 mm. from the preceding set. These are in the middle of the right half sectors (Text-fig. 1, c).

The fourth set is 0.62 mm. from the anterior end and thus 0.24 mm. from the preceding set. They are in the left half sectors very close to the angles of the lumen. These belong to the third type of nucleus, with the extra nucleolus, and probably belong to the angle muscles (Text-fig. 1, d).

The fifth set occurs at 0.88 mm. from the anterior end and 0.26 mm. from the preceding set. Those in the dorsal and left subventral fields are in the right half and very close to the glands. In the right subventral field the nucleus is in the left half and similarly close to the gland (Text-fig. 1, e). They belong to type 1.

The sixth and last set of tear-drop nuclei is at a level about 1.05 mm. from the anterior end and 0.17 mm. from the preceding set. The two in the dorsal and left subventral fields are in the left half and close to the glands; the one in the right subventral field is in the right half and close

to the gland. This set is not far anterior to the end of the cylindrical esophagus (Text-fig. 1, f).

There are 24 nuclei of the cylindrical esophagus referable to the muscles, and all but three of them belong to the surface muscles.

Muscle Nuclei of the Bulb.—The nuclei referable to the anterior bulb muscles consist of a set of three occupying about the middle of the surface fields. They are located at a level near the anterior end. They are of the small rounded type (type 3) (Text-fig. 1, g).

Two types of nuclei are found in the posterior bulb. One of these is of type 1. The other is similar but much larger, 13 μ in diameter. They possess two nucleoli, one spherical and the other blade-like (type 4) (Fig. 38). Their distribution is as follows:

One set of three (type 4), belonging to the angle muscles, is situated 40 to 50 μ from the anterior end of the posterior bulb, one over each angle of the lumen (Text-fig. 1, h). They are in the unmodified section of the musculature.

The second set (type 1) of six nuclei is situated 80 to 90 μ from the anterior end, one in the middle of each half-field (Text-fig. 1, i). They belong to the anterior surface muscles of the corrugated valve. Other nuclei appearing in the figure belong to the esophageal glands and sympathetic nervous system.

The third set consists of six nuclei lying at the level of the anterior surface of the corrugated valve (Text-fig. 1, k). Three are from the surface muscles and three from the angle muscles. The surface nuclei are located far out from the lumen, and belong to the anterior bundles of surface muscles of the corrugated valve. The angle muscle nuclei belong to the anterior bundles of the corrugated valve. All are of type 1.

The fourth set likewise consists of six nuclei, three of which belong to the posterior angle muscles of the corrugated valve, and three to the posterior surface muscles (Text-fig. 1, m). The surface nuclei are of type 1, the angle nuclei of type 4.

Three more nuclei belong to the muscles of the bulb. These are located in the cardia. Their positions shift somewhat, two or even occasionally three being in one cardium; usually they are distributed one to each cardium. Occasionally one or two may be absent, probably due to degeneration with age. They belong to type 1 (Text-fig. 1, o).

This is a total of 24 muscle nuclei in the bulb, of which 9 belong to the angle muscles, the remainder to the surface fields, considering the nuclei of the cardia as belonging to this category. For the entire esophagus there are 51, of four different types. The significance of these types is a problem awaiting solution. I think that some of the reports of nuclei of the esophageal muscles must be erroneous because of failure to make

proper conclusions as to the nature of the nuclei. At the present time nothing can be done to remedy the situation. The correct conclusions must await a considerable volume of comparative work on different forms.

Esophageal Glands.—These structures in Spironoura do not have the extremely high development that they have in the Ascarids. For the greater part of their length they consist of simple tubes (Fig. 18), lacking the complicated branching characteristic of most of the larger parasitic forms. In Spironoura the glands extend from the anterior end of the esophagus to the posterior end, the most complicated branching occurring in the posterior bulb.

From the anterior end to a point about 0.3 mm. posterior to the nerve ring, the tubes are practically unbranched in each field. Here the first considerable branching occurs, forming a labyrinth of gland tissue around and between the muscle fibre bundles, and joining the glandular tissue of the three fields around the angles of the lumen. From this point to the end of the cylindrical esophagus the tubes revert to the unbranched condition. In the anterior end of the anterior bulb the second branched area occurs in a similar manner to the first. Through the remainder of the anterior bulb and the anterior end of the posterior bulb the tube again reverts to an unbranched condition. In the interspaces of the modified muscles of the posterior bulb a third network occurs, here with a much greater bulk of glandular tissue. The basic position of the glands changes here also. Each tube, as it enters the posterior bulb, branches or at least widens toward each side, and the lateral widenings from adjacent surface fields join over the angles of the lumen. In the bulb, the bulk of the glandular tissue is found over these angles. The three nuclei of the glands are found in the same relative positions as are the angle muscle nuclei (Text-fig. 1, i and 1, j). The nuclei are found at about the level of the anterior surface of the corrugated valve, or a little farther anterior. The position of the nuclei over the angles of the lumen, instead of over the flat surfaces, has its parallel in Ascaris (Mueller, 1931). The nuclei are spherical and have a diameter of about 14 μ. The large nucleolus has a diameter of 6 μ.

The openings of the glands apparently are at the same level for all three glandular tubes. This level is the point of junction of the esophagus with the pharynx. At this point the lumen forms three evident outpocketings into which the ducts empty. The openings are in the form of narrow slits (Fig. 45).

Arcade Cells.—Martini (1926) has given an interesting and minute account of these cells in *Oxyuris robusta*. The fundamental structure of the arcade system is the same in *Spironoura chelydrae* as in *Oxyuris*

robusta, but there are variations apparently of a character quite constant for the several species of Spironoura investigated. For the general form of the glands see Fig. 5, drawn from *S. affine.*

There are nine cells in the system, the same number as in Oxyuris. The bodies of these nine cells begin anteriorly at about the anterior end of the pharynx. From this point the arcade cells continue backward a variable distance, but always as far as the nerve ring. The anterior ends are thin and duct-like; the bodies of the cells become progressively thicker posterior to the level of their nuclei, about 30 to 100 μ anterior to the nerve ring, the exact positions varying both individually and for the different cells. Posterior to the nuclei the cells become narrower, and in the case of the dorsal cell, bifurcate.

One of the cells lies against the tissue of the dorsal line. Posterior to the nucleus, as stated above, this cell bifurcates; the two branches following the sides of the dorsal line are wedged in between it and the adjacent muscle cells on each side, one right and one left. Two cells lie over each dorso-lateral angle of the lumen of the esophagus. The ventral one of each of these pairs, while attached anteriorly in this position, bends diagonally ventralward across the lateral line and continues backward at the lower edge of the latter. It is at this point that the nucleus is found. There are two cells over the middle of the ventral muscle fields, one on each side. These are close to the ventral ones of the two pairs just described. The last two cells lie one on each side of the ventral line. The positions of all the cells (at their nuclei) may be seen in Fig. 18. It is clear that this arrangement is essentially the same as that described by Martini (1926) for Oxyuris.

As a matter of convenience, I have described the cells as discrete units. No one of them is, however, independent of the others. A network of cytoplasm interconnects all nine, beginning anterior to their nuclei and continuing nearly to the nerve ring. In Spironoura the arcade system may be considered as a glandular syncytium, forming a more or less complete cylindrical network around the esophagus.

The cytoplasm of the entire syncytium has a very marked staining reaction. It is filled with large spherical granules. In ordinary Delafield-eosin staining of sections, the granules take an intense black, and they are very much overstained when other tissues are about correct. The granules take nuclear stains much more deeply than the nuclei themselves. In toto mounts the best stain is borax-carmine. No stain at all also gives good results, since they are naturally pigmented.

I cannot consider these as amphid glands, although the anterior extremities approach very close to the base of the amphids.

Intestine.—This is the portion of the digestive tract often spoken of

as the "chyle" intestine, and presumably is that portion of the tube in which the actual digestion takes place. In Spironoura the food is probably predigested by the host, so that the function is more absorptive than digestive. The tube is shaped somewhat like a slender baseball bat, with the large end directed forward, and it makes contact with the esophagus in a circular collar (Figs. 3 and 40). It would be useless to give measurements of the diameter of the intestine, since it varies greatly, depending somewhat on the amount of material contained within it, and possibly on factors of contraction. The large end (anterior) may completely fill the entire body cavity and have the posterior bulb partly telescoped into it, causing the walls at the end to be turned in and backward, or it may be no greater in diameter than the bulb and not at all telescoped. The point is mentioned because of the tendency to use measurements of the diameter of the intestine as a specific character.

The shape of the lumen in cross section differs at various levels of the intestine. Anteriorly it is circular, the epithelial cells flattened, and there are no projections into the lumen. At about the level of the junction of the anterior and middle thirds of the tube, the cells of the dorsal and ventral sides of the epithelial lining elongate and become columnar in such a manner as to form a dorsal and ventral projecting ridge corresponding somewhat in shape to the typhlosole in annelids. The ridges reach their maximum thickness at about the middle of the intestine, and here a cross section shows a lumen somewhat in the shape of a letter "N" (Fig. 15). The ridges gradually disappear posteriorly. Just anterior to the rectal sphincter, all the epithelial cells become columnar, and the diameter of the lumen becomes so constricted as to be completely eliminated. This plug of cells is in the nature of a valve into the proctodeum (Fig. 51).

Earlier workers have described the hyaline inner border of the intestinal epithelium as cuticular (Looss, 1905), or as a material accrued from the intestinal contents. Later workers (Hetherington, 1923, and others quoted by him; Mueller, 1929) consider this border to be made up of immobile cilia. In *S. chelydrae* the border is very plain, wide, and distinct, especially in the anterior region. In favorably stained material the transverse striae are clear, and very much suggestive of cilia. (Fig. 50). The distal ends of the cells also frequently show fibres, so as to suggest a neuromotor apparatus, a condition noted by Mueller in Ascaris. No basal granulae were seen, but a thin dark line at the inner borders of the cells may be these structures.

On the other hand, the border does not continue throughout the length of the intestine, being absent posteriorly. If the borders really represent cilia, they must be in a very degenerate condition in Spironoura.

Seen in toto mounts, surface view, the epithelial cells are hexagonal to irregular in shape (Fig. 48). Anteriorly the cell boundaries are distinct, but become less and less so posteriorly, depending somewhat on the staining medium. At about the region of the intestinal sphincter the cell boundaries again become distinct.

The shape of the cells varies considerably according to the amount of fecal material contained in the lumen. All forms from flattened to columnar may be found, and the individual cells vary within limits in this respect.

The nuclei are oval to round, and contain two nucleoli, one of which stains deeply in basic stains, and the other very lightly in the same medium. The position of the nuclei is central or slightly eccentric, near the lumen in columnar cells. The cytoplasm is vacuolar or fibrous according to the stain, and Mallory's triple probably gives the best results (Fig. 48).

As described by Looss (1905) for Ancylostoma, the rectal sphincter has but one nucleus (Fig. 51). The sphincter lies against the rectal ligament posteriorly, in a circular depression around the posterior intestinal plug or valve. Contraction of the sphincter serves to cut off the lumen of the intestine from that of the proctodeum, which could not be accomplished without the aid of the columnar cells of the epithelium. It is possible that the columnar cells are more or less contractile of their own power.

The posterior end of the intestine projects more or less into the proctodeum, posterior to the sphincter. This portion serves as the basis for the connection to the proctodeum, by means of the intestino-rectal ligament to be described later.

Looss (1905), when studying the European hookworm, first described the anastomosis of fibres around the posterior end of the intestine, and commented on what he considered as the probable function of the organ. Except for minor details, his description might have been written for Spironoura, so exactly do the two structures coincide. Looss considered the fibres to be muscles and called them the intestinal muscles.

Just anterior to the rectal sphincter (30 to 40 μ) are found two small nuclei, one on each lateral surface of the intestine and closely applied to the outer wall, that is, to the tunica. A small cytoplasmic body surrounds each nucleus, and radiating out from the central body are numerous fine strands of tissue. These also are applied closely to the tunica. Some run posteriorly and end in or at the anal sphincter, others branch around the intestine dorsally and ventrally, and still others project forward for a distance, in some specimens, of 2 to 3 mm. All of the strands anastomose freely among themselves, and the strands from one

cell anastomose with those from the other. The result is a continuous web of fibres encasing the end of the intestine. In addition, many fibres run across the intervening space of the body cavity to the lateral and median lines, to the ovary or testis, or to the surfaces of the muscle fields. Those around the intestine appear to be encased in a clear hyaline substance, possibly part of the cytoplasm of the two cells, or a secretion of them. The appearance of the muscles in cross section is shown in Fig. 43. This section is cut between the nuclei of the cells and the intestinal sphincter. Since most of the strands in this region are longitudinal the appearance is of discrete longitudinal muscles.

Looss considers these muscles as functioning in forcing fecal matter from the intestine into the proctodeum. An additional function would be the reinforcement of this region of the tract to prevent rupture through too great distention by accumulated contents.

The proctodeum is formed from an invagination of the external cuticula. The invagination becomes covered by a series of external ligament cells, which serve also for support, being attached in various ways to the body wall. The transverse diameter is greater than the dorsoventral diameter, and the anterior end is considerably wider in both dimensions than the posterior end, which narrows to a transverse slit at the anus. The general shape may be seen in Figs. 3 and 19.

The lining is composed of two layers of cuticula. The outer layer is in contact with the ligamentous cells. The inner layer is very thin, little more than a membrane, and is connected only loosely to the outer layer by a reticulum of fine fibres. These fibres are long enough, dorsally and ventrally, to reach approximately half-way across the lumen of the rectum. When the rectum is empty these fibres are extended, and the inner layer of cuticula suspended thus from the dorsum is in contact with that attached to the venter. In this manner the rectal lumen may be completely occluded (Fig. 19).

The entire cuticular wall of the proctodeum is covered externally with a layer of cells (called "ligament" cells by Looss). These cells are in contact with the cuticular wall of the proctodeum and conform to the shape of the outer wall. In addition, certain cells send out processes laterally to form a supportive bridge and dorsally to form a thick mesentery. The boundaries of the cells are sometimes difficult to distinguish, and the nuclei therefore are used to ascertain the cell number, which is apparently ten.

In the female, three of these cells form the intestino-dorsal region of the proctodeum. A thick median process in the sagittal plane projects to the dorsal line, and is firmly secured to it in such a manner as to suggest a thick mesentery (Fig. 19). Each latero-anterior surface is

covered by a large cell, the two meeting ventrally. Lateral projections of these are fused to the lateral lines to form a complete transverse supportive bridge (Fig. 19). The ends of these cells are usually free in nematodes.

The entire proctodeum of the male is a cloaca, since the entrance of the genital canal is almost at the extreme anterior end, and the canal is thus a common duct throughout its length.

As in the female, the anterior end of the rectum is of considerably greater diameter than the posterior end and is dorso-ventrally flattened. The lining cuticula is the same as in the female.

The arrangement of the covering and supportive cells is also the same as in the female, with the following exceptions: (1) There are two cells in the dorsal support (mesentery) instead of one (Fig. 10). (2) The bases of the two cells forming the genital ligament (Fig. 10), and a cell lying between the preanal grooves must be added to the list of ventral cells. This adds four cells to the total, making 14 cells in all.

The genital ligament consists of two cells lying one on each side of the end of the genital tube (Fig. 27). Their posterior ends cover the antero-ventral end of the cloaca. Thus there are five cells in the intestino-proctodeal ligament of the male.

Directly dorsal to the anal opening, and thus at the extreme posterior end of the dorsal wall of the cloaca, an evagination of the cuticula into the body cavity occurs, forming a pocket behind the gubernaculum (Fig. 9). The lumen of this pocket is closed when the spicules are extruded, and slightly open when they are withdrawn. Just anterior to the evagination forming this pocket, a second evagination occurs which is the true spicular canal (Fig. 9). The inner end is open, and the walls lose their cuticular appearance and merge imperceptibly into the gubernaculum posteriorly and into the covering cells of the cloaca anteriorly and laterally. The length of the canal is so negligible as to make the structure little more than a cuticular collar around the ends of the spicules.

The gubernaculum is of a hard, non-pliable material, quite different from the cuticula of the body wall or cloaca. It is, from staining reaction, of the same material as the spicules. In Mallory's triple, both gubernaculum and spicules stain a bright red, while body wall and cloacal cuticula are a light blue. The contrast is quite striking.

In form, the gubernaculum is an oblong flat plate, flaring somewhat at the inner end. The anterior surface is gently concave both laterally and longitudinally; the posterior surface is correspondingly convex. Across the anterior surface above the middle there is a transverse ridge. A corresponding groove across the dorsal surface of the spicules fits

against this ridge, and when the gubernacular muscles close the spicular canal at the bottom, the spicules are tightly held in place by this ridge. On the posterior surface of the gubernaculum is a pointed projection arising near the lower end and curving away from the gubernaculum, much like the barb of a fish hook. This barb is tightly socketed in the anterior wall of the post-gubernacular pocket (Figs. 9 and 10).

The spicules are discussed here because of their intimate structural relation to the cloaca. Their lengths vary from 3.2 mm. to nearly 4.0 mm. When not extruded, the anterior ends lie in the region of the pseudo-sucker, thus being about one-fourth the total body length.

At the anterior end of each spicule is an oval mass of four cells. These lie in the groove formed by the open end on the ventral side. The muscles of the spicule sheath are inserted in the mass of cells posteriorly, and the two retractor muscles have their insertions anteriorly.

The form of the spicule may be seen by observing the cross section (Fig. 46). This section is representative of the structure for most of the length, the two ends, however, varying. The body of the spicule is hollow, and inside the tube is a fibrous tissue. There are two alae, attached laterally, with their edges directed ventrally. The proximal edges of the alae are also hollow. Anteriorly the canals of the alae join the central canal by breaking through the walls. Anterior to this point a cross section resembles a letter "D" with the flat surface on the ventral side. Shortly anterior to this point a portion of the ventral wall disappears. Here the fibrous material inside the canal joins a similar material outside the opening but enveloped in the sheath, and here two nuclei are constantly present (Fig. 44). These perhaps are gland nuclei, and the material inside the tube represents a duct or secretion. The opening in the ventral side of the spicule widens anteriorly until, at the point where the retractor muscles begin, the spicule disappears.

Close to the posterior end of the spicules the lateral alae likewise disappear, leaving only the central body part to form the point. The canals seem to be open at the ends so that any secretion contained within them could be passed to the outside at the posterior tip.

Two retractor muscles of the spicules run forward from the end of each spicule to a point about 2.5 mm. in front of the anterior end of the spicule, where they are inserted in the body wall just dorsal to the lateral line. Each muscle has a single nucleus.

The protractors of the spicules are considerably more complicated. They are attached, as already mentioned, to the anterior spicular cell mass, and also to the rim of the opening in the end of the spicules. They form a continuous sheath around the spicule to the end of the guber-

naculum, where they separate into several bundles, with attachments in the body wall posterior to the gubernaculum on the ventral side, in the lateral body wall, and in the dorsal body wall.

Each branch has a separate nucleus. Since there are four branches, each spicule sheath must be considered as a syncytium of four cells.

Female Reproductive System

As with the majority of nematodes, the ovaries are double in Spironoura; if the condition in free-living forms may be taken as primitive, Spironoura is representative of a condition near that of the primitive nematode. This is not to be considered as meaning a simple condition. Beyond modifications designed to facilitate quantity production, the primitive condition is apt to be more complex than that found in parasitic forms of long standing. Quantity production of embryos or eggs is often associated with loss or atrophy of certain organs. Thus in Dracunculus, there is a complete loss of all muscular organs of the uterus, glandular epithelium, and all the vagina, in late adult stages.

General Description.—The length of each ovary in *Spironoura chelydrae* (counting uterus, glands, etc., but not vagina) is roughly twice the entire body length. The vagina is 3.5 to 4.5 mm., or somewhat less than one-third the total body length. This length is extraordinary when compared with other species of the genus. In *S. catesbieanae* the vagina is less than 0.5 mm. long, and in *S. affine* it may reach a length of 1.25 mm., which two figures represent the minimum and maximum of all other North American species.

While the length of the tubes is in no way comparable to forms like Ascaris, it is nevertheless great enough to make it very difficult to follow the tubes through in toto mounts of the entire worm and to determine the exact disposition of the organs located. Longitudinal sections afford the best studies, not only of gross structure but also of histological details. I have had recourse also to dissections, and in favorable instances, I was able to remove and disentangle the entire genital system.

The extremity of the anterior ovary (Fig. 56) lies a short distance posterior to the posterior bulb of the esophagus (a). Figs. 56 and 53 show the gross morphology of both the tubes. The coils here are more or less constant for all species of the genus which I have studied, the greatest variation resulting from the shorter vagina in the other species.

Histology of the Female System.—The extremity of each ovary is capped by an apical cell (Fig. 29). Around it is a thin membrane, which also covers the entire ovary, becoming modified in the more proximal sections. This membrane is nucleated (Fig. 28), apparently is a

syncytium in the distal part, and is evidently a true epithelium. It is exceedingly thin at the free (distal) extremity, not exceeding 1 μ in thickness. It thickens proximally, and the cells become spindle-shaped, the long axis of the spindle coinciding with the long axis of the tube. The bodies of the cells project inwardly into the lumen of the ovary, giving in cross section the appearance of longitudinal muscle fibres lying along the inner surface of the ovarian membrane (Fig. 28).

Some 20 to 30 μ from the apical cell the true ovarian epithelium may be seen, composed of columnar cells projecting at an angle into the lumen of the tube. The primordial germ cells, which may be seen in the tube at this point and farther along, are produced from the epithelium.

The gametes are characteristically formed in various parts of the tube of the ovary. Those nearest the apical cell, recognizable as germ cells, are oval or round, about 4 μ in diameter (greatest), with a distinct large nucleus. Next is a region of mitotic activity, which produces oögonia that become progressively smaller toward the proximal end of the tube. The reduction in size takes place largely in the cytoplasm, while the nuclei become rather irregular in shape (Fig. 31). The reduction in size continues for only a short distance.

Up to this point in the tube (about 0.5 mm. from the end) no rachis is visible. Between this point and a point 0.3 mm. farther along, the cells become visibly larger; this increase in size continues to the end of the ovary, where the cells have reached their maximum bulk, not counting the shell material. At about the region where the growth in the oöcytes begins, a distinct rachis becomes visible. It is formed from strands left trailing behind the gametes as they move along the tube. Even before the central rachis is visible as such, isolated strands may be observed among the gametes. Soon after the rachis is formed the gametes become radially arranged around it, each cell assuming a more or less triangular shape, with the acute angle toward the rachis (Fig. 26). Here it might be noted that what appears in cross section to be a regular radial pattern, is in reality spiral in form; as may be seen from study of longitudinal sections and toto mounts. The edges of the cells overlap, so that the cell boundaries in cross section become more and more difficult to see. In the more proximal regions of the rachis tube this overlapping gives the appearance of a syncytium.

At first the rachis is straight, following the center of the tube. Farther down, where the cells have become large enough to fill more than half the tube, it begins to zigzag from side to side (Fig. 53). The overlapping gradually becomes more pronounced, and the final result is that the cells become large enough to fill the entire width of the tube, and proceed henceforward in single file. The most pronounced pressure is

now in the direction of the long axis of the ovary; hence the cells assume the form of circular flat plates (Figs. 21 and 28). In fully mature females the rate of production of eggs becomes so great that the cells become flattened to such an extent that the nuclei may bulge out on both sides.

The portion of the tube not productive of oögonia is technically oviduct, although for reasons of convenience I have made no distinction, there being no definite separating point. At the end of the oviduct is a short constricted region, the function of which is evident. Although not much longer than an egg (about 0.2 mm.), the gametes pass into it in the form of a flat plate and emerge in the typical oval "egg" shape, which is retained henceforward. A columnar epithelium lines the inside of the constriction, replacing the spindle cells of the oviduct. The cells are here angled sharply toward the proximal end of the genital tube, and probably serve somewhat as a valve to prevent movement backward, and partly as a mold for the eggs. Since the structure of the cells resembles that of the cells of the shell gland, it will not be described here.

It is necessary to point out that the designation of the next part of the tube as shell gland is subject to question. Looss (1905) considered a similar organ in Ancylostoma as more in the nature of a vitellarian gland, and considered the uterus as the functional shell gland. There is considerable evidence to support his conclusions. On the other hand, I have studied the cytoplasm of the cells entering the gland and those leaving it, and can detect no difference which would indicate an added food supply. Certainly there is no added bulk. There is a refractive, mucus-like layer around the eggs as they emerge from the gland. It is my opinion that this substance during subsequent passage through the uterus hardens into a shell. In the semi-liquid state, while in the inner end of the uterus, it would not prevent passage of the sperm in fertilization. I think it altogether probable that the uterus elaborates some substance that serves to harden the shell.

The shell gland is a relatively short portion of the tube. The diameter depends on the activity, presence of eggs, etc., but it is usually rather narrower than the oviduct. The outer epithelium presents no special modifications. The lining is composed of a series of epithelial cells of columnar form, the cytoplasm of which is filled with numerous large spherical vacuoles. The basal cytoplasm is finely granular, and the boundaries of the cells indistinct. No evident cell boundaries are to be seen in the lumenward ends, and discrete strands of cytoplasm may often be seen in the lumen (Fig. 23). The nuclei are small and situated near the base of the cells.

Spermatozoa are most numerous in the extreme inner end of the

uterus near the junction with the shell gland. This region is in no way different in structure from the remainder of the uterus, but it seems advantageous to designate it as "seminal receptacle" simply to call attention to the sperm present. Penetration of the eggs by the sperm takes place here. The wall of the uterus has a totally different arrangement from any described portion of the tube. Around the outside is an arrangement of circular contractile cells; the lining is composed of a low epithelium, which is, however, structurally quite different from the epithelium of the shell gland. It also has a different staining capacity.

The outer muscular layer is composed of spindle-shaped cells, broad and flat on the inner side applied to the epithelium and with quite apparent longitudinal (transverse to the longitudinal axis of the tube) ridges running most of their length around the outside. The appearance of these ridges, which contain the nuclei of the cells, when seen in toto mounts, suggests discrete circular bands (Fig. 56), and the bases of the cells appear to be a middle layer. Sections (especially longitudinal) show the true relation of the parts. At the inner end of the uterus one muscle cell is sufficient to reach most of the way around the tube, especially when in a state of contraction; this increases the impression of complete bands. At the end adjoining the vagina the cells are much shorter, while the diameter of the tube is larger, so that as many as three or four cells are necessary to complete the circumference. This is not to be taken to mean that the ends of the cells abut each other in a truncate manner. The cells are spindles, more or less sharply pointed at each end, and overlap the ends of the cells on each side. The arrangement, therefore, is more spiral than circular. Cell boundaries are very indistinct in cross sections (Fig. 35) and toto mounts, but show plainly in longitudinal sections.

The epithelium consists of oblong flattened cells, in the middle of each of which is an irregular cytoplasmic lobe into the lumen. The longitudinal axis of these cells corresponds to the longitudinal axis of the tube; therefore, it is at right angles to the outer layer of muscle cells. The inner cytoplasmic lobes contain the nuclei (Fig. 35). A large quantity of mucous material is elaborated by this epithelium, the function of which is, partly at least, to lubricate the passage of the eggs. Quantities of the substance are passed on into the vagina with the eggs.

The appearance of the cytoplasm is quite different from that of the shell gland epithelium. The numerous vacuoles are absent, and the cytoplasm is dense and homogeneous.

Vagina.—This portion of the genital tube differs from the uterus in two quite apparent ways. First, the epithelial lining is absent, and its place is taken by a cuticular lining; second, the spiral of muscle cells

around the outside have their surfaces reversed, that is, the contractile lamellae are outside, at least the heavier portion, and the cytoplasmic cell bodies containing the nuclei are inside and completely surrounded by contractile substance (Fig. 2). In general arrangement, the muscle cells resemble those of the uterus. They are spindles encircling the outside of the tube, with the ends of the cells overlapping; the arrangement is, therefore, spiral and has much the same appearance as the uterus, except that the muscle bands never appear to be separated. They are evidently much more powerful in contractions than the uterine muscles. The muscles are attached loosely to the inner cuticular lining by means of radially arranged connective tissue fibres (Fig. 30). The same fibres attach the cells to each other laterally, allowing independent movement, which is a necessity when the cells are spirally arranged. Only two nuclei occupy the fibres, both near the vulva (Fig. 2).

Near the inner end of the vagina the lumen is regularly circular in cross section. Toward the vulva, however, in the absence of eggs, the lumen has a regular cross or diamond shape (Fig. 30). The cuticula is composed of eight longitudinal plates, joined to each other laterally; when an egg is passing through, the plates have the appearance of a continuous circular piece; when the tube contains no eggs, the lumen is constricted and the cuticula bends inward at each alternate joint, while the others bend outward. Because of the intervening connective tissue fibres, it is not necessary for the muscle cells to conform to the shape of the cuticular lining.

At the junction of the vagina with the body wall at the vulva, there is a modification of the ventral line to form a peculiar pad-like organ surrounding the end of the vagina. This may possibly be, as sometimes described, an organ glandular in nature. The arrangement of the cells is shown in Fig. 2. I incline to consider it a purely mechanical buffer. A special vulvar ganglion lies just posterior and to one side of the pad, which is usually called the "vaginal gland." That the pad has some special significance is evidenced by the exceptional number of large nuclei in it—about four on each side and behind, and at least a dozen anterior to the vulva. The pad is separated from the ventral line tissue, and the nuclei are of different form. No ducts of any kind could be found.

Between the end of the spiral muscles of the vagina and the vaginal gland there is a very large sphincter muscle surrounding the cuticular lining. This is a single-celled organ (Fig. 2).

Male Reproductive System

Genital Tube.—Like the ovary in the female, the testis of the male begins with a single apical cell (Fig. 32). This extremity lies posterior to the ventral sucker, the exact position depending somewhat on the state of maturity of the individual. From the apical cell the testis runs forward to a level a short distance posterior to the posterior esophageal bulb (Fig. 12), whence the tube turns backward. About the middle of the body the testis ends. It is followed by a large sac-like seminal vesical continuous posteriorly with the seminal gland. The latter is nearly a third as long as the body, the posterior extremity lying about midway between the pseudo-sucker and the cloaca. Here the tube is again constricted, and at the posterior end of the constriction is a valve, opening into a peculiar muscular area which I am calling the ejaculatory duct. The latter is divided into two evidently different portions, the proximal portion being glandular as well as muscular. The posterior extremity of the ejaculatory duct joins the cloaca ventrally near the anterior end, and it is held in place by the genital ligament.

The male genital tube is thus divided into five quite different portions: (1) testis, (2) seminal vesicle, (3) seminal gland, (4) valve, and (5) ejaculatory duct, which latter is itself subdivided. If the proximal portion of the testis be considered as vas deferens, then there are six morphologically different parts of the tube. This is evidently a greater number than has been recognized for the majority of nematode species. Note that in this species there is no organ comparable to the ejaculatory duct of some species in which the walls are enveloped by *circular* muscles.

Testis.—Anatomically the testis corresponds very closely to the ovary of the female. The extremities of the two tubes are almost identical, though some differences are noticeable at the proximal end in contact with the seminal vesicle. The apical cell at the distal extremity of the testis is possibly somewhat smaller in proportion than the apical cell of the ovary (Fig. 32). The outer epithelium at the extremity is composed of an exceedingly thin cellular layer, and lined with a low germinal epithelium. This latter is usually indistinguishable from the germ cells within the lumen, so tightly is the entire mass packed into the tube.

The outer epithelium gradually changes in character from the distal to the proximal end of the testis. Beginning as a thin membrane, the cells become more and more elongate and spindle-shaped, their long axes corresponding almost to the longitudinal axis of the tube. These spindle cells never become absolutely longitudinal, but are arranged in long spiral rows around the testis. Tangential longitudinal sections are necessary

to show this peculiarity. Such sections also show the contractile fibres to best advantage. As in the ovaries, the cytoplasmic non-contractile bodies of the cells project into the lumen (Fig. 34).

A short distance from the apical cell, the germinal epithelium disappears as a definite lining layer. At about the point of disappearance the spermatogonia begin to show a definite increase in size, which is progressive to the end of the testis. The cells form around a rachis, attaining as in the ovary a definite radial disposition (Fig. 34). This arrangement is retained to the end of the testis, and the spermatocytes never attain a size comparable to that of the oöcytes.

Seminal Vesicle.—This portion of the tube is generally spoken of as a storage region (Fig. 12), but that is not its principal function. Here occur the peculiar reducing phenomena common among nematodes. Temporary storage may take place, but if it does, it is probably in the ejaculatory duct.

The walls of the seminal vesicle consist of only a simple flattened epithelium. There is no lining epithelium.

Seminal Gland.—I have hesitated to call this gland a cement gland. There is no evidence that its secretion is used to seal the male to the female during copulation as in some nematodes. In the absence of any real knowledge concerning its function, I prefer the noncommittal term *seminal gland*. The epithelium lining this part of the tube is evidently productive of a large amount of mucous material, but whether or not it is nutritive is an unsettled question.

The structure of the seminal gland is almost an exact equivalent of the cement gland of Ancylostoma as described by Looss (1905). The epithelium is columnar and very highly vacuolated, and the cells incline in the tube toward the proximal end. The lumen is usually obliterated by the ends of the cells. In general the structure is very much like the shell gland of the female. The secretion stains a light blue with Mallory's triple, both in the lumen and in the vacuoles. As in the shell gland of the female the best studies are afforded by longitudinal sections (Fig. 25). All the nuclei are crowded near to the basal region of the cells, in some cases being in contact with the thin outer epithelium, which does not differ from that of the seminal vesicle.

Between the seminal gland and the labyrinthine tube of the ductus ejaculatorius, there is a narrowly constricted region. The proximal end of this region contains fibrous epithelial cells of a columnar shape, arranged so that their lumenward ends extend into the labyrinthine tube. This forms a sort of a one-way valve evidently designed to prevent backward movement of the sperm in the tube. The arrangement of the cells is shown in Fig. 24.

Ductus Ejaculatorius.—The valve described above opens directly into a portion of the genital tube with a very interesting structure. The entire canal consists of a reticulum of muscular fibres anastomosing in every direction (Fig. 24). The spermatozoa pass through the spaces in the reticulum; thus they must here take a very irregular course. Nuclei are scattered here and there through the fibres of the reticulum, but are usually found near the periphery. The entire tissue is a complicated syncytium. Near the middle of the ductus ejaculatorius, glandular epithelial cells replace most of the contractile fibres, and become more numerous toward the proximal end. The nature of their secretion is also problematical. With iron hematoxylin or mordanted Delafield's hematoxylin the vacuoles and droplets in the reticular spaces stain a deep blue or black (Fig. 36). Lacking the hematoxylin, they will stain with eosin.

At the end of the ejaculatory duct is a very short tube composed of flattened epithelium. This region is entirely encased by two large ligamentous cells, one on each side and joining each other dorsally and ventrally. The posterior ends of these two cells are continuous with the ligamentous cells suspending and covering the cloaca. Their function is to form a connection between the genital tube and the lumen of the cloaca. These cells I am calling the *genital ligament* (Fig. 27).

The accessory reproductive organs of the male (special muscles, spicules, gubernaculum, and posterior papillae) are discussed in connection with the systems with which they are associated.

Musculature

As in all oxyuroids, the musculature is meromyarian and platymyarian. The total number of somatic cells is 132. These are divided equally among the four fields, thus 33 in each. Each field has 16 cells in the row adjacent to the median lines, and 17 in the row adjacent to the lateral line. Details of their form and arrangement differ from the ordinary condition as described for such forms as Ancylostoma, Ascaris, and Oxyuris, or for any other with which I am acquainted. The differences will be noted as described.

At the anterior extremity two cells from each field have their insertions in the thickenings of the ring support of the lips, that is, in the angle supports and the pharyngeal supports. These eight cells (designated as half-cells by Martini) are truncate at their anterior ends and are markedly shorter than the following cells.

The second set of eight cells have their anterior ends near the posterior end of the pharynx. From here to the level of the esophageal bulb, four cells may always be seen in cross section in each muscle field.

More, of course, may be seen if the cross section is taken near the ends of the cells where overlapping occurs. Fibres from the second set of eight cells form the septum muscularis.

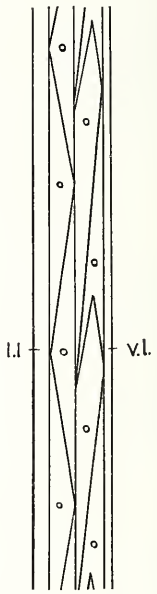
The somatic muscle cells have two quite different forms. This is a modification I have not met with elsewhere. Alternate cells in each field, in the rows adjacent to the ventral and dorsal lines, are bifurcate at the posterior extremity and single pointed anteriorly (Text-fig. 2). All the remainder of the cells are spindles, but not in any case "rhomboids" as described by Martini (1916) for Oxyuris. The bifurcate cells have the anterior point at the median lines, and one of the posterior points at the ventral (or dorsal) line and one at the submedian line. The cell of the same row just behind it has the anterior point in the split end of the bifurcate cell anterior to it and the posterior point at the ventral line, wedged in between the ventral line and the anterior point of the next posterior bifurcate cell.

The cells of the rows adjacent to the lateral lines on each side have also a unique arrangement. Both ends of each cell are adjacent to either the submedian line or to the lateral line, alternating in this respect throughout the length of the row. All these cells are therefore triangular, with a very long base against a submedian or lateral line and with the other two sides equal and much shorter.

It is clear that none of these cells could be described as rhomboids although the rather indefinite term "spindle" might fit any but the bifurcate type.

Mueller (1929) described some inclusions within the cytoplasm near the extremities of the muscle cells in Ascaris. In some of the cells in Spironoura, in a similar position, a single large body nearly as large as the nucleolus, may frequently be seen. Most of these are to be found in the anterior body region. They stain very deeply by Heidenhain's method.

In addition to the bodies apparently confined to the extremities of the cells, any number of other cytoplasmic inclusions of various sizes and position may be found in any of the cells (Fig. 54). These apparently will not stain without mordanting with iron alum. Using this mordant with



TEXT-FIG. 2.—Schema of the somatic musculature. *l.l.*, lateral line; *v.l.*, ventral line.

Delafield's hematoxylin, and countering with eosin, one may stain these inclusions black, the general cytoplasm a purplish blue, and the contractile lamellae red.

The contractile lamellae in cross section appear as a letter "U" (Fig. 59), with the open end turned toward the hypoderm. The ends of the arms of the "U" may be bifurcate also.

The anal muscles are referable to the "H" type as described by Martini (1916) for Oxyuris, i.e., a double vertical row inserted dorsally between the dorsal edge of the lateral lines, and ventrally on either side of the ventral line posterior to the anus and in the dorsal side of the rectum. The two rows are connected by a transverse cytoplasmic bridge containing a nucleus. The system is much more highly developed in the male than in the female. The entire series of strands is referable to a single cell in the female; to several cells in the male.

Accessory Muscles of the Male.—The pseudo-sucker of the male lies just anterior to the ventral oblique muscles and doubtless represents a modification of these. It probably does not represent a true sucker, yet it seems likely that it is a functioning organ. I find it difficult to consider the structure as a degenerate organ; I think it much more likely that it represents an organ in process of development (phylogenetically) by means of concentration of fibres.

The muscles of the pseudo-sucker consist of 22 or 24 pairs of fibres, each single strand representing a single cell, the ventral ends of which are inserted in or near the midventral line. The dorsal insertions are in the lateral body wall on either side between the ventral edge of the lateral line and the dorsal edge of the subventral longitudinal muscle fields (Fig. 58). The ventral insertions are grouped close together, the dorsal ends considerably farther apart, so that the whole group of muscles on one side has the general shape of a fan. The longitudinal muscle bands of the subventral fields pass under the pseudo-sucker muscles, that is, between them and the body wall.

The ventral insertions are arranged in such manner that they form an oblong oval, the long axis coinciding with that of the long axis of the body. The ventral line lifts up from the body wall and passes over the base of the insertions and between the strands of either side.

Each separate muscle strand contains a nucleus, which occurs about two-thirds of the distance from the ventral end. They do not lie in the contractile fibres but in a bulge of non-contractile cytoplasm on the inner surface. This cytoplasm is granular and alveolar, and usually contains several small bodies which stain very much like the nucleolus and appear like small nuclei. These cells are distinctly like the somatic muscle cells

in general arrangement. At the insertions each muscle may break up into several strands which have the appearance of a frayed end of a rope.

The ventral oblique muscles are in all respects like the pseudo-sucker muscles, except that they are all inserted exactly in the midventral line. The fibres from the two sides mix into a network at the body wall, and the cells are parallel (Fig. 58). The muscles begin at the anterior extremity of the preanal grooves and end at the posterior edge of the pseudo-sucker. The fibres of the anterior end of each muscle are attached obliquely forward from the ventral insertions. The few anterior muscles cross the posterior ends of the pseudo-sucker muscles. The ventral obliques number from 42 to 44 pairs.

Accessory Somatic Musculature of the Male.—Because the male has a set of muscles not present in the female, it is necessary to discuss a part of the somatic system as distinct from the female system. All somatic elements of the female are present in the male also, but in addition the male has a field of cells lying between the ventral edge of the lateral lines on each side and the dorsal row of ordinary somatic muscle cells of the subventral fields (Fig. 58). I call this additional field of cells the accessory somatic muscles of the male. Seurat (1918) mentions this system of muscles. The cells of this accessory field are only about one-sixth as broad as the ordinary somatic muscle cells, but are longer proportionately, being about half the length of the ordinary somatics. At the widest part (just anterior to the cloaca) the accessory fields are about six cells wide, and the individual cells are here somewhat wider than those at the anterior extremity. The bands end anteriorly at about the level of the esophageal bulb, and posteriorly near the anus.

The course of the individual cells is somewhat variable. Anterior to the pseudo-sucker, the anterior ends are either at the edge of the lateral lines or at the edge of the ordinary somatic muscle fields. The posterior ends are at about the middle of the bands. At the level of the pseudo-sucker they become more regular in their arrangement. The anterior ends are at the dorsal edge of the ordinary somatic muscle field. The posterior ends are at the edge of the ventral border of the lateral lines; thus their course is diagonal to the long axis of the body. The effect of this arrangement probably is to counter the ventral oblique bands which cross the accessory bands at an acute angle.

Excretory System

In general organization the excretory system in Spironoura belongs to the "X" type as described by Martini (1916) for *Oxyuris curvula*. In details it varies from any of the described systems. The excretory bridge

is regularly composed of three cells forming a syncytial longitudinal bar, beneath which the four canals meet at the excretory pore. The space beneath the bar appears in toto mounts like a large bladder.

The interior of the excretory canals usually is filled with a finely granular material which stains with almost any ordinary cytoplasmic stain. In toto mounts the material may be seen to be concentrated at odd points along the tubes, sometimes in sufficient quantity to cause slight distention.

Studies on the excretory canals in living specimens have yielded some interesting points of information. Slightly immature specimens were used, since they are more transparent. Specimens were placed on a slide in normal saline solution or water, wedged in between two cover slips, and covered with a third slip. This prevents excessive motion, and many details of internal anatomy are clearly visible. The excretory canals may be traced from end to end. At the level of the proctodeum, i.e., the posterior extremity, the tube may be seen to pulsate, widening slowly like a filling bladder and then contracting to such an extent that the lumen is obliterated. The fluid contents may be seen to move forward under impetus of the contraction of the bladder, and a form of peristaltic wave along the tube. Obviously the thickened wall of the posterior end is contractile.

While the excretory pore is visible, no fluid could be seen issuing from it as a result of contraction of the bladder. However, because of limited material, these observations are as yet inconclusive and need to be repeated.

III. DESCRIPTIONS OF NEW SPECIES

Genus Spironoura Leidy 1856

Diagnosis.—With the characters of the subfamily Kathlaniinae. Small to medium-sized worms attenuated at each extremity. Head truncate, with three low lips, sometimes partially divided. The lips each bear two bifurcate papillae, the inner branches ending in a small papillus on the inner surfaces of the lips, the outer branches ending in a larger papillus on the anterior surfaces of the lips. A pair of low flattened amphids present, one on each side of the head in close approximation with one of the anterior branches of the subventral lip papillae. Cervical papillae far posterior, nearly at the level of the excretory pore, and consisting of a projecting spherical knob.

Around the base of the vestibule is an internal ring of cuticular nature, with three nodes or thickenings, one in the middle of each lip,

serving for the attachment of the lip muscles (above) and pharyngeal muscles (below), and with three additional nodes, each one supporting an angle of the lumen of the vestibule, and thus binding the lips together.

Cuticula without alae, plectanes, or other modifications or thickenings. Transverse striations extremely minute.

Tail in both sexes conical, acute.

Muscular pharynx present, clearly separated from the esophagus. Lumen of the esophagus with accessory canals at the angles. Esophagus with a posterior bulb equipped with a mobile corrugated valve and intestinal valve (cardia), and constricted anterior to the middle, thus being divided into a small "anterior" bulb and a larger "posterior" bulb.

Intestine expanded anteriorly, gradually attenuated posteriorly, and equipped internally with dorsal and ventral ridges, resembling the typhlosole of annelids.

Proctodeum pyriform, expanded anteriorly and usually greater in diameter than the posterior end of the intestine; suspended dorsally and laterally to the dorsal and lateral lines respectively, each "mesentery" being composed of a single cell (except in the "dorsal mesentery" of the male in which there are two).

Excretory system of the "X" type, the bridge consisting of a longitudinal bar of a syncytium of three cells, under which a space giving the impression of a bladder (the pseudo-bladder).

Vulva of the female located near the junction of the middle and posterior thirds of the body. Vagina directed dorsally and anteriorly from the vulva; muscular, and lined with cuticula. Uteri opposite; ovaries with ends directed one anteriad and the other posteriad. Shell glands present between ovaries and uteri.

Male spicules variable in length, alate and acute. Gubernaculum present, sometimes incompletely cuticularized. Caudal papillae consisting of three pairs of preanal subventrals, three pairs of circum-anal subventrals, and a variable number of postanals; usually two pairs of subventrals and two pairs of laterals.

Male usually with a pseudo-sucker; sometimes four, sometimes none. Always with a series of precloacal oblique muscles posterior to the pseudo-sucker, and an accessory polymyarian muscle field between the meromyarian ventral somatics and the lateral line.

Tip of the testis near the posterior end of the body; one ascending and one descending loop to the genital tube; entire system ventral (or partially lateral) to the digestive tube. Seminal vesicle, seminal gland (cement gland), and ductus ejaculatorius present.

Parasites of turtles (usually) or other reptiles, and amphibia, and fishes (rarely).

Synonyms: Spirura Diesing 1861; Falcaustra Lane 1915; Florencioia Travassos 1919; Spectatus Travassos 1923; and doubtfully, pending further investigation, Zanclophorus Baylis and Daubney 1922.

Spironoura wardi n. sp.

I have made several collections of this species, which is quite distinctive from any other described species. The host is *Chelydra serpentina.* As yet I have discovered it in no other species of turtle, but in view of the variable host adaptability of other North American Spironourans, I judge it will be found in other hosts sooner or later. The species is named in honor of Dr. Henry B. Ward, Professor of Zoology in the University of Illinois.

Diagnosis.—With the characters of the genus. Measurements in Table 2. The angle nodes of the lip support ring have characteristic horn-like points directed obliquely outward (Fig. 67). The pharyngeal supports are rather weakly developed, as are the connecting bars. There is nothing especially characteristic about the head papillae, lips, etc. Arcade glands with so little pigment as to be invisible in ordinary toto mounts. The cylindrical esophagus is thickest at about the middle. Both bulbs are almost perfectly spherical (Fig. 8). The pseudo-bladder is rather long, the posterior end about even with the middle of the posterior bulb in large specimens, farther forward in smaller specimens, and somewhat variable according to the contraction of the esophagus, body wall, etc. The pore is one-third of the length of the bladder from the anterior end.

The tip of the anterior ovary of the female lies far back of the posterior bulb, and the tip of the posterior ovary may reach the rectum. The posterior shell gland reaches to the vulva anteriorly, and the anterior shell gland lies rather far forward of the vulva. The vagina is extraordinarily long compared with spicule length (Table 2). The greatest body width of the female usually lies immediately in front of the vulva, in contrast with other species in which the greatest body width is usually near the junction of the middle and anterior thirds of the body. The body of a mature female is always abruptly narrower just posterior to the vulva.

The characters of the male are more distinctive. There are 35 to 40 pairs of muscles in the precloacal obliques, and 40 to 48 pairs in the pseudo-sucker. This is the only North American species in which the pseudo-sucker contains more muscles than the precloacal oblique system.

The male caudal papillae (Fig. 6) are arranged as follows: Two pairs of postanal subventrals are located close together about two-thirds of the length of the tail from the anus. At a level between these two is a lateral pair. Another lateral pair is located just posterior to the level of the anus.

A third pair of subventral postanal papillae is located at a level about one-third of the length of the tail posterior to the anus. Note that this pair does not occur on any other North American species, excepting *S. longispicula* (Walton) 1927.

The circum-anal papillae consist of three pairs, the anterior two of which are located very close together at the level of the anus, and the third pair slightly posterior to the anus.

There are three pairs of preanal subventral papillae, the posterior pair of which lies at about the anterior end of the cloaca, sometimes anterior to it, and sometimes posterior; rather variable in position. The middle pair always lies shortly anterior to the level of the anterior end of the spicules (when retracted). The anterior pair lies slightly more anterior to the middle pair than the middle pair is anterior to the posterior pair.

In all there are 11 pairs of caudal papillae and a single precloacal papillus in front of the anus.

TABLE 2.—MEASUREMENTS OF APPROXIMATELY MAXIMUM AND MINIMUM MATURE SPECIMENS (IN MILLIMETERS)

Spironoura wardi Mackin 1936

Females	Minimum	Maximum	Males	Minimum	Maximum
Total length	7.98	13.72	Total length	6.81	8.41
Greatest breadth	0.29	0.47	Greatest breadth	0.25	0.33
Head breadth	0.06	0.11	Head breadth	0.09	0.09
Breadth at anus	0.16	0.24	Breadth at anus	0.16	0.17
Pharynx length	0.06	0.07	Pharynx length	0.05	0.06
Pharynx breadth	0.07	0.08	Pharynx breadth	0.05	0.05
Cylindric esophagus length	1.18	1.47	Cylindric esophagus length	0.93	1.32
Cylindric esophagus breadth	0.08	0.10	Cylindric esophagus breadth	0.07	0.08
Anterior bulb length	0.12	0.14	Anterior bulb length	0.10	0.11
Anterior bulb breadth	0.11	0.13	Anterior bulb breadth	0.09	0.11
Posterior bulb length	0.15	0.20	Posterior bulb length	0.13	0.16
Posterior bulb breadth	0.17	0.20	Posterior bulb breadth	0.14	0.16
To excretory pore	1.00	1.38	To excretory pore	0.77	1.17
To nerve ring	0.30	0.35	To nerve ring	0.26	0.33
Rectum length	0.16	0.22	Cloaca length	0.12	0.17
To vulva	5.13	8.12	Sucker to anus	1.02	1.51
Vagina length	0.80	1.08	Spicule length	0.33	0.37
Tail length	0.53	0.79	Tail length	0.28	0.41
Eggs length	0.079	0.099	Gubernaculum length	0.07	0.08
Eggs breadth	0.059	0.060			

The tip of the testis in *S. wardi* usually lies at about the anterior end of the ductus ejaculatorius (mature specimens). The ductus is longer than usual and clearly separable into three regions.

This species is most closely related to *Spironoura testudinis* (Baylis and Daubney) 1922. The arrangement of the male caudal papillae is almost identical in the two species. *S. wardi* differs from *S. testudinis* most markedly in possessing a pseudo-sucker, and also in having much shorter spicules.

Type host: *Chelydra serpentina,* snapping turtle.

Type locality: Southeastern Oklahoma.

Type material: In the collection of Dr. Henry B. Ward, University of Illinois, Urbana, Illinois.

Spironoura concinnae n. sp.

Two collections of worms taken from the rectum of *Pseudemys concinna* I am designating as representing a new species. More than a hundred specimens, all of which were mature, were taken in the two collections. Mounted specimens of the same species I found in the collection of Dr. Henry B. Ward, University of Illinois, from Illinois (same host).

Diagnosis.—With the characters of the genus. Measurements are given in Table 3. Unfortunately I have been able to make only two collections of this species, in both of which all specimens have been nearly of the same size range. All specimens are fully mature and may represent the approximate limit of growth. Smaller specimens are needed to complete data on the growth range and to give some idea of variations in the relative size of different organs during growth. Out of nearly a hundred specimens the females vary hardly more than a millimeter; the males, however, vary as much as five millimeters.

Head structure is shown in Figs. 68 and 69. Characters of specific value are difficult to point out, but attention may be called to the exceptional height of the lips and the very robust papillae stalks. The lips are, of course, subject to variation according to fixation and contraction of the muscles.

In the development of the arcade glands and pigmentation of the esophagus *S. concinnae* approaches *S. affine.* However, the arcade cells extend back in *S. concinnae* hardly farther than the nerve ring, while in *S. affine* they extend far beyond the ring.

Measurements of the esophagus coincide quite closely with those of *S. wardi,* but the shapes of the two bulbs are quite distinctive (Fig. 11). The posterior bulb in *S. concinnae* is more nearly pyriform than spheri-

cal, and the greatest diameter is posterior to the middle. The constrictions between the bulbs, and between the anterior bulb and the cylindrical esophagus, are shallow, so that the bulbs lack a rounded appearance.

The posterior end of the pseudo-bladder lies beside the anterior bulb and the excretory pore far forward in the bladder, about one-fourth the length of the bladder from the anterior end. In lateral view, the nuclei of the bridge cells form a triangle; the posterior two lie at about the middle, one dorsal to the other, and the third nucleus lies near the anterior end.

While in most species of Spironoura the measurements of the tail are not very good specific characters, in *S. concinnae* the length is extraordinary enough to warrant its use in such capacity. The relative length is considerably greater than in any other species (Table 3).

In the female the ovaries have a tendency to form a series of coils near the extremities; hence the tips are relatively far from the esophageal bulb and the rectum. The tendency to coil is not to be found in all individuals to the same degree. It is not due to crowding, since all of the body cavity space is not utilized.

In the males the tip of the testis extends posteriorly but little farther than the pseudo-sucker. A characteristic feature of the males is the very heavily developed and long ductus ejaculatorius, which extends almost to the pseudo-sucker. In a 13 mm. male this structure is 2.1 mm. long.

TABLE 3.—MEASUREMENTS OF APPROXIMATELY MINIMUM AND MAXIMUM MATURE SPECIMENS (IN MILLIMETERS)

Spironoura concinnae Mackin 1936

Females	Minimum	Maximum	Males	Minimum	Maximum
Total length	14.6	15.8	Total length	8.69	13.4
Maximum breadth	0.47	0.54	Maximum breadth	0.34	0.38
Breadth at anus	0.21	0.23	Breadth at anus	0.17	0.20
Pharynx length	0.07	0.07	Pharynx length	0.07	0.08
Pharynx breadth	0.07	0.08	Pharynx breadth	0.07	0.07
Cylindric esophagus length	1.47	1.60	Cylindric esophagus length	1.30	1.42
Cylindric esophagus breadth	0.12	0.14	Cylindric esophagus breadth	0.11	0.11
Anterior bulb length	0.14	0.16	Anterior bulb length	0.12	0.13
Anterior bulb breadth	0.13	0.14	Anterior bulb breadth	0.11	0.12
Posterior bulb length	0.18	0.21	Posterior bulb length	0.18	0.19
Posterior bulb breadth	0.18	0.19	Posterior bulb breadth	0.17	0.18
To excretory pore	1.36	1.42	To excretory pore	1.15	1.22
To nerve ring	0.33	0.36	To nerve ring	0.33	0.36
Rectum length	0.23	0.24	Cloaca length	0.26	0.28
To vulva	8.93	9.40	Sucker to anus	3.00	3.33
Vagina length	0.99	1.06	Spicule length	1.07	1.15
Tail length	1.02	1.25	Tail length	0.46	0.52
Eggs length	0.086	0.099	Gubernaculum length	0.15	0.16
Eggs breadth	0.059	0.066			

There are from 45 to 52 pairs of oblique muscles in the precloaca and from 25 to 32 pairs in the pseudo-sucker. Note that these figures separate this species quite definitely from *S. affine,* a closely related form.

The spicules extend only about one-third of the distance from the anus to the pseudo-sucker when retracted, and are less than half the length of the ductus ejaculatorius.

The subventral postanal papillae (Fig. 66) consist of two pairs which lie at a level two-thirds to three-fourths of the tail length posterior to the anus. At the same level is a lateral pair. A second lateral pair lies just posterior to the level of the anus.

Usually the 3 pairs of circum-anal papillae are all slightly posterior to the anal opening, although the anterior pair may be at the level of the anus or even, rarely, slightly anterior to it.

The first pair of preanals lies between the levels of the middle and anterior end of the cloaca. The second pair is rather variable, usually lying just anterior to the middle of the spicule, and sometimes forward of this point. The third pair lies anterior to the end of the spicule, sometimes only slightly so, or even with the end.

The papillae in *S. concinnae* are exceptionally small and often very difficult to see. In some specimens I have been unable to locate the anterior preanal pair, even when all the other papillae were clearly visible. It may be that this pair is actually not present in some specimens, which would not be an unusual condition.

This species has its nearest relative in *Spironoura procera* Canavan 1929. It differs from this species in the possession of a well-developed pseudo-sucker.

Type host: *Pseudemys concinna.*

Localities: Southeastern Oklahoma; Illinois.

Type specimens in the collection of Dr. Henry B. Ward, University of Illinois, Urbana, Illinois.

Key to the North American Species of Spironoura

1 (2) Without a pseudo-sucker.....*Spironoura procera* Canavan 1929.

2 (1) With a pseudo-sucker..... 3

3 (6) Male with 11 pairs of caudal papillae..... 4

4 (5) Pseudo-sucker of the male with 40 to 48 pairs of muscles; spicules not longer than 0.37 mm. in length.....*S. wardi* Mackin 1936. (Figs. 6, 8, 65, and 67)

5 (4) Pseudo-sucker weakly developed; spicules 1.2 to 1.21 mm. in length.....*S. longispicula* (Walton) 1927.

6 (3) With ten pairs of caudal papillae in the male..... 7

7 (8) Head with a series of grooves originating at the angles between the lips and spiraling part-way around the head; anterior bulb of the esophagus long, narrow, cylindrical...*S. cryptobranchi* Walton 1930. (Figs. 4, 7, and 14)

8 (7) Head without spiral grooves; anterior bulb inflated..... 9

9 (10) Spicules very long, 2.35 to 4.5 mm.....*S. chelydrae* (Harwood) 1932. (Figs. 3, 10, 12, 17, and 20)

10 (9) Spicules not longer than 1.2 mm..... 11

11 (12) Spicules not longer than 0.3 mm.; pseudo-sucker with 11 or 12 pairs of muscles.....*S. catesbeianae* (Walton) 1929. (Figs. 13, 60, 62, and 63)

12 (11) Spicules from 0.9 to 1.2 mm. in length..... 13

13 (14) Entire pseudo-bladder and excretory bridge anterior to the anterior end of the anterior esophageal bulb; 39 to 40 pairs of muscles in the ventral oblique muscles of the male.....*S. affine* Leidy 1856. (Figs. 1, 5, 61, and 64)

14 (13) Posterior end of the pseudo-bladder and the excretory bridge at the level of the anterior esophageal bulb or posterior to it; 45 to 52 pairs of muscles in the ventral oblique system of the male..... .....*S. concinnae* Mackin 1936. (Figs. 11, 66, 68, and 69)

Note: No attempt has been made to key *S. gracile* Leidy 1856 since not enough specific information is available to separate it from several other North American species.

IV. OBSERVATIONS ON GROWTH AND VARIATION

This study was undertaken primarily to test the value of formulae designed to aid in the separation of species of nematodes. Such formulae are based on measurements of various body regions or organs, and are expressed as percentages of the total body length (or width). N. A. Cobb has been the chief advocate of the use of what has become known as "Cobb's formula," and has used his own formula extensively, especially in descriptions of free-living nematodes.

Growth in *Spironoura chelydrae*.—This species was selected as a basis for study for no other reason than that a wealth of material was available; certainly a necessary condition for such a study. Twenty-five specimens were measured, and each measurement computed as a percentage of total body length. The specimens were selected to cover as nearly as possible the entire size range of the species, from immature specimens to the largest mature specimen available. Only females were used, and the minimum range extended only as far as specimens in which the vulva was easily discernible. Table 4 shows the results of the measurements. The worms are numbered from I to XXV, the first being the smallest, the last the largest, and the others ranging in as nearly

evenly graded steps as possible. Only a few of the major divisions of the body were measured: the region between the anterior extremity and the level of the posterior end of the esophagus (including the bulb), the region from bulb to vulva, the region from anterior extremity to vulva, from vulva to anus, and from anus to posterior tip (tail). For each of these regions, the length in millimeters is given in the left column, and the percentage of the body length in the adjacent column to the right. At the bottom of each column of measurements is given the percentage of growth of that particular body region as computed from the smallest and largest specimens.

The first point of interest lies in the exceptionally great range in actual total size of the species. The first six specimens and the eighth specimen were sexually immature. This leaves the range of mature females from 8.68 to 22.55 mm., easily the greatest range in size of any species of Spironoura described. Some of the mature specimens of any other species of Spironoura at present described would fall within this range.

The most significant fact brought out by the measurements is the variability of percentages of different body regions to the total length. In the smallest specimen, for instance, the esophagus is 24.4 percent of the total length. In the first few immature individuals this percentage is increased, and apparently has a maximum in specimens in the 6-mm. range (27 to 29 percent of the total body length). From that point on to the maximum sized specimens the percentage decreases, until the esophagus represents only 11.7 percent of the total length. Thus while the esophagus is actually steadily increasing in size, its relative length as steadily decreases. The esophagus actually grows 105.3 percent (computed from the increase in size over the smallest specimen).

At the same time that region of the body between the bulb and the vulva grows from 2.14 mm. in length to 11.03 mm.—an increase in size of 415.4 percent. In the smallest specimen this region is 40.5 percent of the total length, and the percentage *increases* up to 48.9 in the largest specimen.

No additional discussion is necessary for other body regions. The relative position of the vulva is most constant; the tail is variable (not related to growth) to such an extent that not much may be said concerning it. The factor of most importance is that different body regions and organs very evidently do not grow at the same rate, even after the specimens are fully mature sexually. From these studies it is clear that the use of formulae based on percentages must be of very limited value. Their usefulness would depend entirely on coincidence (by different in-

TABLE 4.—MEASUREMENTS AND PERCENTAGES OF THE TOTAL BODY LENGTH OF VARIOUS BODY PARTS OF THE FEMALE *Spironoura chelydrae* (Harwood) 1932

Specimen number	To posterior end of bulb		From bulb to vulva		From anterior end to vulva		From vulva to anus		Tail length		Total
	mm.	%	mm.	%	mm.	%	mm.	%	mm.	%	mm.
I[1, 3]	1.29	24.4	2.14	40.5	3.43	64.9	1.41	26.7	0.44	8.33	5.28
II[1, 3]	1.84	29.5	2.43	37.7	4.27	67.2	1.58	24.9	0.50	7.86	6.36
III[1, 2]	1.74	27.14	2.626	41.0	4.36	68.1	1.51	23.6	0.52	8.23	6.41
IV[1, 2]	1.84	28.6	2.534	39.2	4.38	67.8	1.55	23.9	0.52	8.27	6.46
V[1, 2]	1.79	24.8	3.055	42.2	4.85	67.0	1.90	26.2	0.47	6.56	7.23
VI[1, 2]	1.68	19.3	4.15	48.65	5.83	67.95	2.22	25.9	0.52	6.15	8.58
VII[2]	1.84	21.1	3.80	43.8	5.64	64.9	2.38	27.5	0.66	7.60	8.68
VIII[1, 2]	1.9	21.5	4.01	45.5	5.91	67.0	2.37	27.0	0.52	5.99	8.81
IX[2]	1.9	20.0	4.33	45.36	6.23	65.36	2.64	27.7	0.66	6.90	9.53
X[3]	2.03	21.1	4.17	43.4	6.2	64.5	2.64	27.5	0.76	7.91	9.60
XI[3]	1.92	19.6	4.54	47.1	6.46	66.7	2.62	26.6	0.66	6.77	9.74
XII[3]	1.95	18.4	4.29	46.0	6.84	64.4	3.57	28.8	0.71	6.69	10.6
XIII[3]	2.00	18.5	5.31	49.0	7.31	67.5	2.82	26.1	0.68	6.34	10.8
XIV[3]	1.71	14.9	5.57	48.6	7.28	63.5	3.53	30.8	0.66	5.52	11.45
XV[3]	1.79	14.7	6.12	50.2	7.92	64.9	3.67	30.1	0.60	4.97	12.19
XVI[3]	1.98	15.4	6.33	49.5	8.31	64.9	3.71	29.0	0.76	6.00	12.8
XVII[3]	1.84	14.0	6.73	51.6	8.58	65.6	3.77	28.8	0.71	5.44	13.06
XVIII[3]	2.08	14.3	7.287	50.2	9.37	64.5	4.46	30.6	0.68	4.72	14.52
XIX[4]	2.16	13.6	7.69	48.8	9.85	62.4	4.54	28.7	1.39	8.80	15.79
XX[4]	2.32	13.9	8.16	47.9	10.48	62.8	4.18	25.0	1.42	8.50	16.68
XXI[4]	2.34	13.3	9.15	52.0	11.49	65.3	4.61	26.2	1.48	8.40	17.58
XXII[4]	2.43	12.9	9.94	52.7	12.37	65.6	4.91	26.09	1.55	8.10	18.83
XXIII[4]	2.64	13.7	10.03	52.1	12.67	65.8	5.15	26.7	1.42	7.40	19.25
XXIV[4]	2.66	12.7	10.48	51.7	13.14	64.4	5.43	26.6	1.82	8.90	20.40
XXV[4]	2.64	11.7	11.03	48.9	13.68	60.6	7.23	32.5	1.64	7.27	22.55
Percentage of growth	105.3	....	415.4	....	298.8	....	412.7	....	272.7	....	327.0

[1]Immature specimens. [2]From the host *Pseudemys elegans*. [3]From the host *Chelydra serpentina*. [4]From the host *Macrachelys temminchii*.

vestigators) in collecting specimens of a certain species which would be of approximately the same growth stage or size.

There is evidence that the species and size of the host may have something to do with regulating the size that a parasitic species may attain. Table 4 will illustrate this point. The smallest mature specimens of *Spironoura chelydrae* which I have been able to collect have come from *Pseudemys elegans*. Specimens VII and IX of the table came from this host (as well as some of the immature specimens). The mature individuals up to number XVIII all came from *Chelydra serpentina*. Specimens XIX to XXV all came from the alligator snapper turtle, *Macrachelys temminchii*. It is not clear whether these specimens range larger than specimens from other host species because of the difference in species, or whether the difference in size is due to the larger size of the host. All of the specimens listed in the table from *Macrachelys temminchii* were from a single host specimen which weighed approximately 100 pounds. Whatever the reason, the fact remains that the size of the parasites differs radically in different hosts.

Mention may be made here concerning the growth of the hard substances designated as "cuticular," or "chitinous." Organs of such nature are generally accepted to be secreted material and thus non-cellular. I have already called attention to the fact that these substances are not cuticular, and that they are generally understood not to be of chitin. Many workers apparently consider variation in size of such structures to be of limited nature, and the variation less than for cellular organs. They therefore use measurements of these structures more constantly than measurements of other structures, in specific diagnosis. The spicule of the male is an example. Actually such organs grow, in many cases, proportionately with cellular organs. It is not surprising that this should be so, since the size of spicules is a reflection of the activity of the cells which secrete them, and which are presumably active throughout the growth period of the individual. The advantage in use of such structures does not lie in the lack of variability in size, but in the fact that, being of hard substance, they are less liable to distortion in killing, fixation, etc.

Obviously some revision or modification of existing methods of specific description of nematodes is desirable. In order to clarify the problem, more critical separation of generic from specific characters is necessary.

I have estimated, from a thorough study of specific descriptions of North American species of Spironoura, that roughly 40 percent of the characters given are generic in value and thus entail that amount of wasted space in description. When such measurements, given without

due regard for variational range or maturity of specimens, are coupled with almost valueless specific characters and poor illustrations, it is quite apparent why confusion of species so commonly occurs.

V. SUMMARY

The nematode species *Spironoura chelydrae* (Harwood) 1932 (Oxyuroidea, Kathlaniidae) has been made the subject of extended anatomical studies. Special attention has been paid to the histology of the arcade system, the entire digestive tract, the genital systems, and the supportive (non-cellular) structures of the head. Analyses of the esophagus for nuclear position, type, and constancy show these considerations to be generic in extent. A new type of somatic musculature, concerning gross cell shape and arrangement, has been described.

A careful analysis of the basis for separating species by means of "nematode formulae" has shown that this method is practically valueless, and is a source of much confusion. The analysis consists of a study of growth in *Spironoura chelydrae* covering the entire range in size. Percentages of length of various body regions in all stages of growth have been computed. These percentages vary widely in the different stages, showing that growth is radically unequal when comparing different sections. It is clear that formulae for different growth stages would vary beyond the limits of usability. In addition, it is pointed out that limits of growth are determined, to some extent at least, by the host species. Lastly, contraction plays a more important rôle in variation than has heretofore been considered possible.

Two new species have been described, *Spironoura wardi* and *Spironoura concinnae*. A key for the separation of the North American species has been compiled.

EXPLANATION OF PLATES

Abbreviations

a....amphid
ab....anterior bulb
ac....accessor canal
am....angle muscles
amu...anal muscles
an....angle node
ao....anterior ovary
ar....arcade cells
asm...anterior fibres of the surface muscles of the corrugated valve
asr....anterior subcuticular ring
b.....bar connecting angle node and pharyngeal node
cb....collar of the bulb
ct.....connective tissue
de....ductus ejaculatorius
dg....dorsal gland
dl.....dorsal line
ds....dorsal support of the rectum
dsm...dorsal spicular muscle
eb....excretory bridge
ed....excretory duct
eg....esophageal gland
ep....epithelial plug
epe...external papillus ending
epo...excretory pore
gl.....genital ligament
gm....gubernacular muscles
gp....glandular portion of the ejaculatory duct
gr....head grooves
i.....intestine
im....intestinal muscles
ip....internal papillus ending
is.....intestinal sphincter
ll.....lateral line
lm....lip muscles
ls.....lateral support cell
lsm...lateral surface muscles of the pharynx
mc....muscles of the cardia
mr....muscular reticulum of the ejaculatory duct
ms....median strand
msm...median surface muscle
n.....nerve cell
nr....nerve ring
p.....pharynx
pb....pseudo-bladder
pc....primary cuticula
peb...posterior excretory bridge
pg....preanal groove
pgp...post-gubernacular pocket
pn....pharyngeal node
po....posterior ovary
pp....preanal papillus
ps....pseudo-sucker
psm...posterior fibres of the surface muscles of the corrugated valve
pt....pharyngeal tooth
r.....rectum
sc.....spicular canal
sec....secondary cuticula
seg....seminal gland
sev....seminal vesicle
sf.....somatic muscle fibres
sg....shell gland
sm....surface muscles
t.....testis
tr.....transverse lip ridge
v.....vestibule
va....vagina
vag...vaginal glands
vas....vaginal sphincter
vl.....ventral line
vs.....ventral support cell of the rectum
vsm...ventral spicular muscles
vu....vulva

PLATE I

FIG. 1.—*Spironoura affine.* Anterior body region from a toto mount stained in Ehrlich's hematoxylin. Scale equals 0.1 mm.

FIG. 2.—*Spironoura chelydrae.* Longitudinal sagittal section through the vulva, showing vaginal sphincter, vaginal gland, muscles, etc. Stained in Mallory's triple.

FIG. 3.—*Spironoura chelydrae.* Female, from a toto mount stained in Lyon's blue. Not all of the genital tubes shown. Scale equals 0.2 mm.

FIG. 4.—*Spironoura cryptobranchi.* Ventral view of head from a lactic acid mount. Free-hand.

FIG. 5.—*Spironoura affine.* Anterior extremity stained with borax carmine. Details, except for arcade system, omitted. Free-hand.

FIG. 6.—*Spironoura wardi.* Tail of male. From a toto mount stained in Ehrlich's hematoxylin. Scale equals 0.1 mm.

FIG. 7.—*Spironoura cryptobranchi.* Tail of male. From a cleared specimen of type. Scale equals 0.1 mm.

FIG. 8.—*Spironoura wardi.* Anterior body region from a toto mount stained in methylene blue (70% alcoholic solution). Scale equals 0.1 mm.

FIG. 9.—*Spironoura chelydrae.* Sagittal section through the cloacal region of the male. The section is exactly in the median plane ventrally, but to one side of the median dorsally. A combination of several sections as far as the muscles of the gubernaculum and spicules are concerned. Stained in Mallory's triple. Details omitted.

FIG. 10.—*Spironoura chelydrae.* Tail of male from a toto mount stained in methylene blue (alcoholic solution). Anterior two pairs of preanal papillae not shown.

FIG. 11.—*Spironoura concinnae.* Anterior body region from a toto mount stained in methylene blue (alcoholic solution). Scale equals 0.1 mm.

FIG. 12.—*Spironoura chelydrae.* Male, from a toto mount stained in indigo carmine. Scale equals 0.2 mm.

FIG. 13.—*Spironoura catesbeianae.* From a toto mount of one of the paratypes. Scale equals 0.1 mm.

FIG. 14.—*Spironoura cryptobranchi.* Esophageal bulb from a type specimen. Scale equals 0.1 mm.

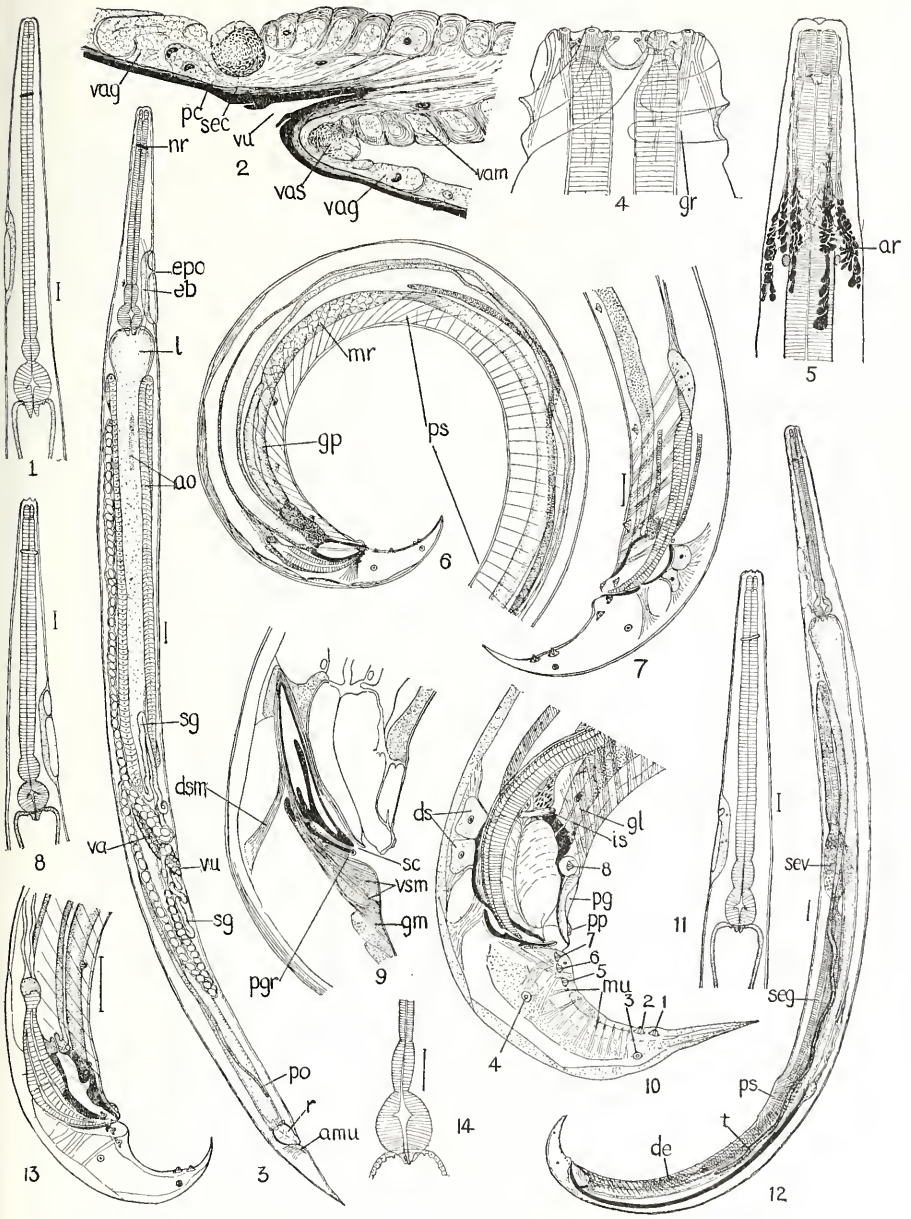

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PLATE I

PLATE II

Spironoura chelydrae

FIG. 15.—Section through the middle region of the intestine, showing dorsal and ventral ridges. Mordanted Delafield's and eosin.

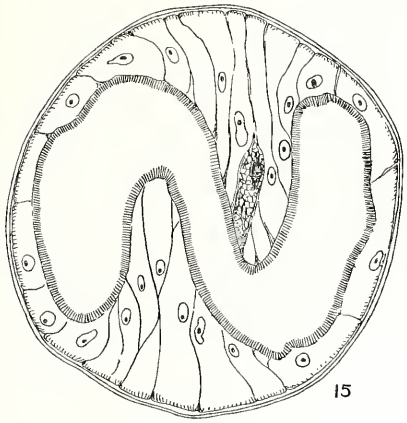
FIG. 16.—Section through the anterior esophageal bulb, showing the excretory ducts and bridge. Also nerve cells in the subventral esophageal glands of the anterior bulb.

FIG. 17.—Face view of head cleared in lactic acid. Free-hand.

FIG. 18.—Section through the cylindrical esophagus anterior to the nerve ring. Heidenhain's. From a single section except for the nuclei of the arcade cells. Only two of these actually appear in the section drawn; others in adjoining sections.

FIG. 19.—Section through the rectal region of the female to show ligament cells. Delafield's and eosin.

FIG. 20.—Ventral view of the head from a lactic acid mount. Free-hand.



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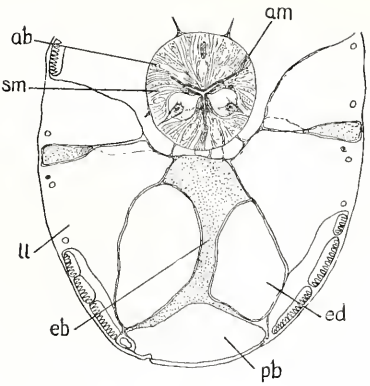

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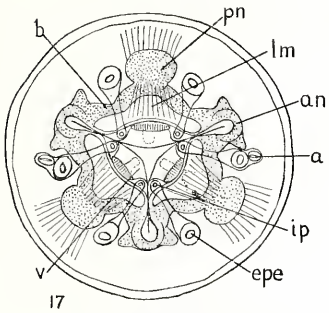

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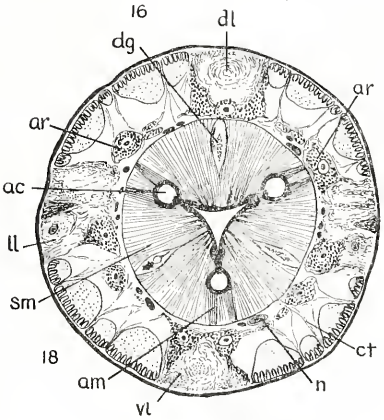

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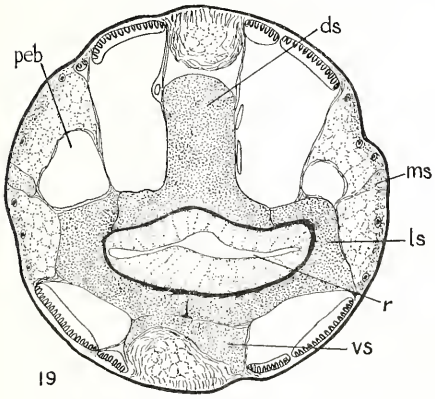

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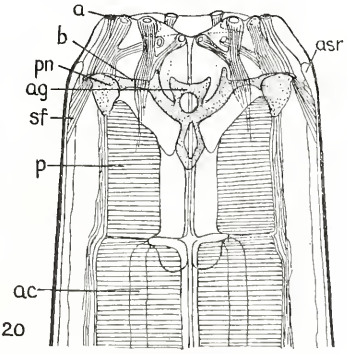

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PLATE II

PLATE III

Spironoura chelydrae

FIG. 21.—Longitudinal section of proximal end of an ovary. Mallory's triple.
FIG. 22.—Chromosomes from a fertilized egg. Heidenhain's.
FIG. 23.—Longitudinal section through the shell gland. Mallory's triple.
FIG. 24.—Longitudinal section through the genital valve and distal end of the ductus ejaculatorius. Mordanted Delafield's and eosin.
FIG. 25.—Longitudinal section through the seminal gland of the male. Mallory's triple.
FIG. 26.—Cross section of ovary near the distal end showing rachis.
FIG. 27.—Section through the genital ligament of the male.
FIG. 28.—Transverse section through the ovary; about the same region as Fig. 21. Delafield's and eosin.
FIG. 29.—Transverse section through the apical cell of the ovary.
FIG. 30.—Transverse section through the vagina.
FIG. 31.—Transverse section through the ovary in the region of the oögonia.
FIG. 32.—Longitudinal section through the apical cell of the testis.
FIG. 33.—Transverse section through the ovary near the tip, showing primordial germ cells.
FIG. 34.—Transverse section through the testis near the proximal end. Rachis present.
FIG. 35.—Transverse section through the uterus.
FIG. 36.—Longitudinal section through a portion of the wall of the ductus ejaculatorius to show secretions. Oil immersion. Heidenhain's with eosin. Free-hand.

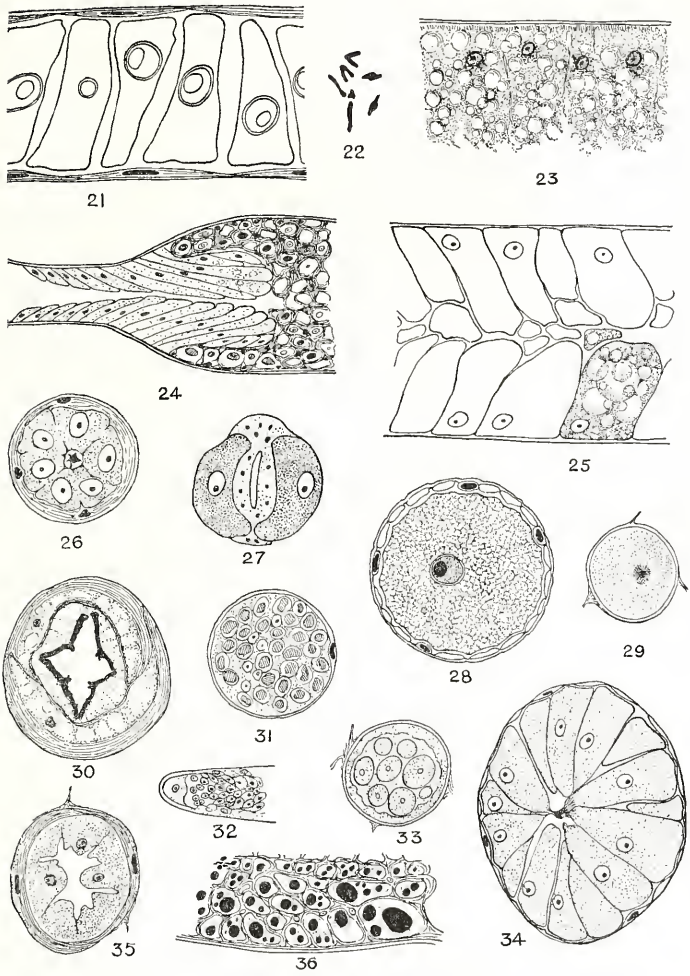

PLATE III

PLATE IV

Spironoura chelydrae

FIG. 37.—Angle muscle nucleus of the cylindrical esophagus. Oil immersion. Heidenhain's with eosin. Free-hand. Type 3.

FIG. 38.—Muscle nucleus from the posterior bulb. Oil immersion. Heidenhain's. Type 4.

FIG. 39.—Surface muscle nucleus of the cylindrical esophagus. Oil immersion. Heidenhain's. Type 1.

FIG. 40.—Longitudinal section through a dorsal cardium to show muscles and collar of the bulb.

FIG. 41.—Transverse section through the corrugated valve.

FIG. 42.—Surface muscle nucleus of the cylindrical esophagus and bulb. Oil immersion. Type 2.

FIG. 43.—Transverse section through the posterior region of the intestine to show the intestinal muscles.

FIG. 44.—Section of a spicule near the posterior end to show the gland nuclei.

FIG. 45.—Duct of the dorsal gland. Oil immersion.

FIG. 46.—Section of a spicule near the middle.

FIG. 47.—Transverse section through the pharynx.

FIG. 48.—Tangential section through the intestine to show form of the epithelial cells. Mallory's triple. Oil immersion.

FIG. 49.—Frontal section through the posterior esophageal bulb, somewhat ventral to the middle to show musculature.

FIG. 50.—Transverse section of intestinal cells to show stiff cilia. Oil immersion. Heidenhain's.

FIG. 51.—Transverse section through the intestinal sphincter.

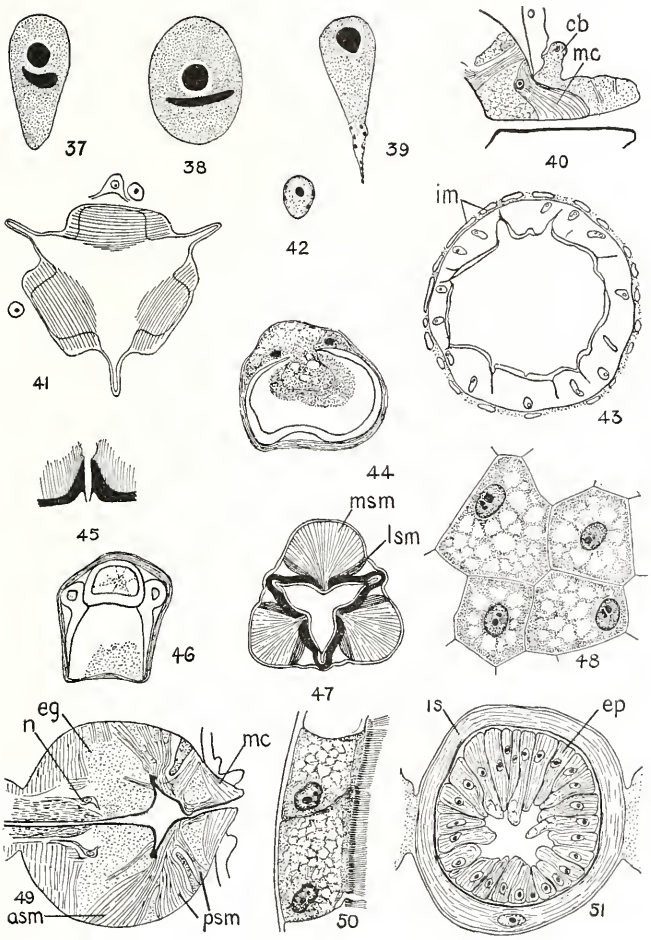
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PLATE IV

PLATE V

Spironoura chelydrae

FIG. 52.—Longitudinal section through the head and pharynx; somewhat to one side of sagittal, through the dorsal lip.

FIG. 53.—Posterior ovarian system. Coils somewhat spread apart so that all details may be seen.

FIG. 54.—Longitudinal section of a somatic muscle cell to show cytoplasmic inclusions. Oil immersion. Free-hand.

FIG. 56.—Anterior ovarian system from a dissection.

FIG. 57.—Lateral view of the angle node of the lip support ring. Free-hand from a lactic acid mount.

FIG. 58.—The pseudo-sucker, oblique ventrals, and accessory muscle fields of the male. From a dissection stained in borax-carmine. Partly diagrammatic.

FIG. 59.—Transverse section of a somatic muscle cell, to show the form of the contractile lamellae. Oil immersion. Free-hand.

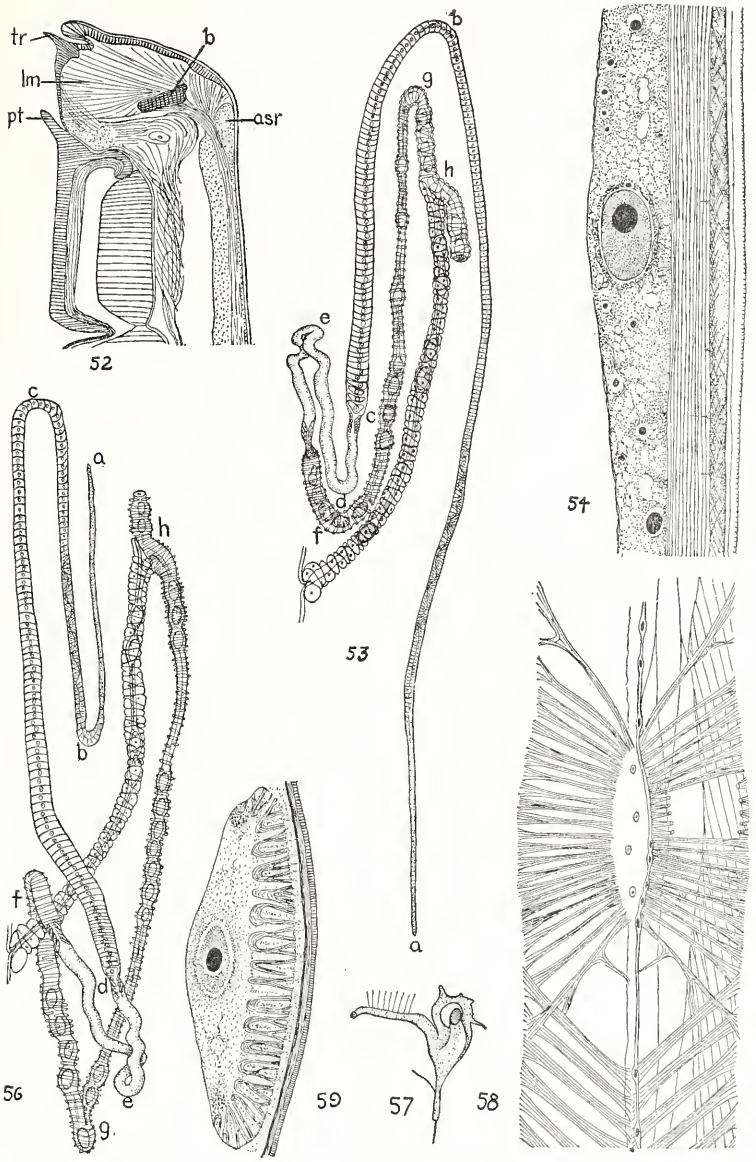


PLATE V

PLATE VI

FIG. 60.—*Spironoura catesbieanae.* Ventral view of the head from a lactic acid mount.

FIG. 61.—*Spironoura affine.* Anterior view of the head from a lactic acid mount.

FIG. 62.—*Spironoura catesbieanae.* Anterior view of the head from a lactic acid mount.

FIG. 63.—*Spironoura catesbieanae.* Anterior body region. Scale equals 0.1 mm.

FIG. 64.—*Spironoura affine.* Ventral view of the head from a lactic acid mount.

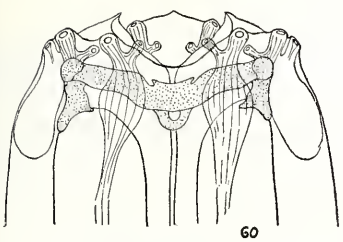
FIG. 65.—*Spironoura wardi.* Ventral view of the head from a lactic acid mount.

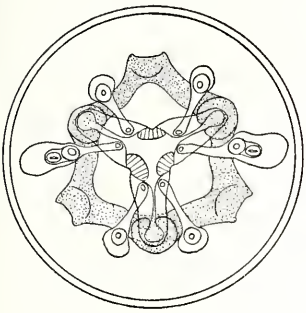
FIG. 66.—*Spironoura concinnae.* Tail of the male.

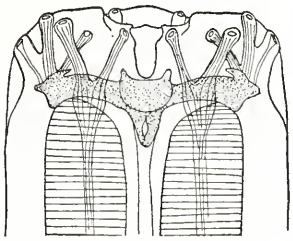
FIG. 67.—*Spironoura wardi.* Anterior view of the head from a toto mount in lactic acid.

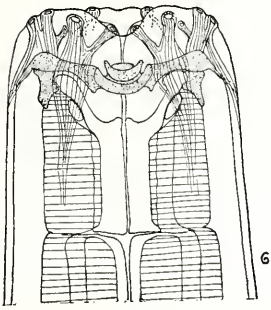
FIG. 68.—*Spironoura concinnae.* Ventral view of the head from a lactic acid mount.

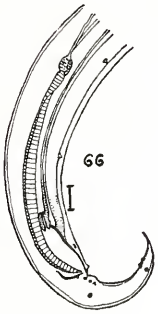
FIG. 69.—*Spironoura concinnae.* Anterior view of the head from a lactic acid mount.

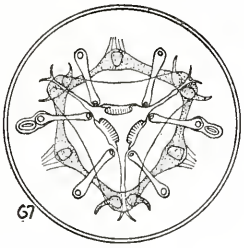


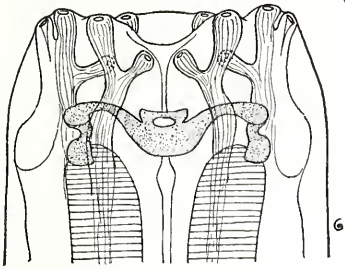












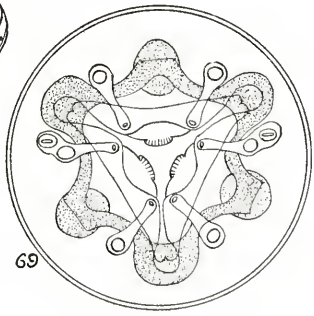


PLATE VI

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